

Growth, Mortality and Movements of a Sanctuary Population of Maskinonge (*Esox masquinongy* Mitchell)^{1,2,3}

By E. J. CROSSMAN⁴

University of Toronto, Toronto 5, Ontario

ABSTRACT

A Schumacher population estimate based on 995 maskinonge taken by trap nets, between the months of May and October in the years 1951–1953, set the number of maskinonge in Nogies Creek at between 769 and 1,122 in July 1953. The mean standard length of these fish was 53.0 cm. The rate of growth (26.3 cm. S.L. in the first year) compared favourably with that for maskinonge in other waters. Fish of age-groups II, III and IV predominated. The small number of fish over four years of age was apparently due to a 70% annual mortality rate at least after the third year of life and perhaps before age III.

Recaptures of tagged maskinonge demonstrated that there was little movement of maskinonge in summer, and what movement there was, was mainly upstream. In the fall there was far more movement of fish, and this was mainly in a downstream direction.

The area supports a fairly large population of maskinonge but the high mortality after three years of age limits its value for raising maskinonge to legal size. The potential for rearing fish to three years of age is such that it may be very advantageous to move hatchery fish here for one or two years before liberation.

INTRODUCTION

Because the Kawartha Lakes of Ontario support a heavy sport fishery for maskinonge, it was considered that the population of this species in the Nogies Creek Sanctuary, part of the system, could in some way aid in supporting this heavy pressure on the lakes. To assess the value of the fish in the sanctuary an investigation was begun in May 1951.

Nogies Creek is in Galway and Harvey townships of Peterborough county. Nogies Creek, from the foot of Bass Lake to the outlet of Big Marsh, is a fish sanctuary maintained by the Ontario Department of Lands and Forests. The sanctuary consists of an 80 acre lake with a mean depth of eight feet, and four miles of meandering stream 20–30 yards wide with a mean depth of approximately 10 feet. The part of the sanctuary studied consisted of the lake (Big Marsh) and approximately one mile of the stream north to Watson's bridge (Fig. 1).

The nature of the stream made it closed to immigration and emigration and since as a sanctuary it was closed to angling, the population of fish in this body

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⁴Author's present address: c/o Institute of Fisheries, University of British Columbia, Vancouver 8, B.C.

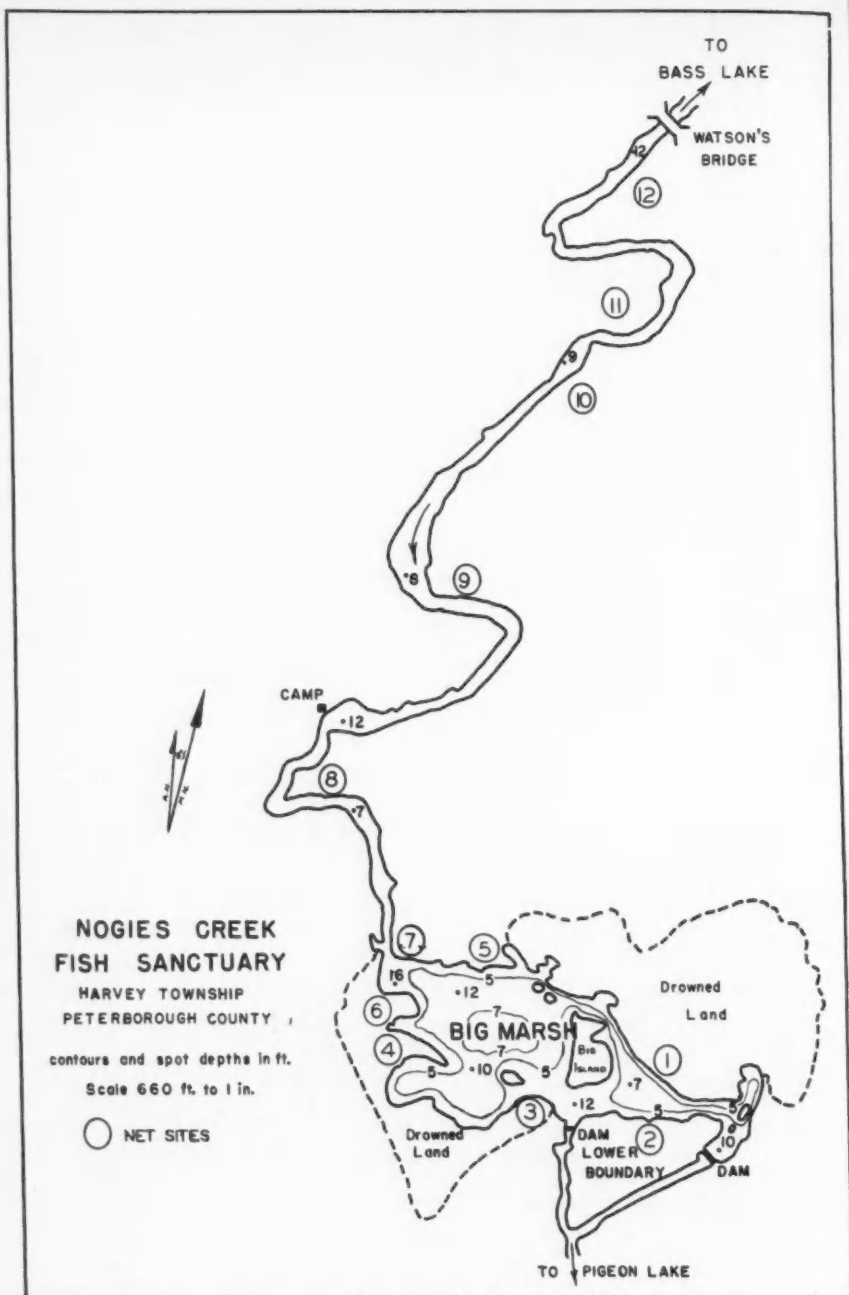


FIG. 1.—Map of the section of Nogies Creek Fish Sanctuary studied.

of water was unexploited. Loss of fish through causes other than natural mortality was negligible.

METHODS AND MATERIALS

Maskinonge were taken by means of trap nets from the early part of May to the early part of July in the years 1951-1953. In 1952 and 1953 nets were set for approximately 15 days in October in order to transplant fish to other lakes. Netting sites are shown in Figure 1. Two sizes of nets were used:—six-foot trap nets with traps of two inch mesh and 100 foot leads of two and one-half inch mesh, and eight foot nets of two inch mesh with 150 foot leads of two and one-half inch mesh.

In 1951, fin clipping was used to identify captured fish. A cut approximately one inch deep was made in the trailing edge of a fin and this portion of the fin torn away along a fin ray. This method, rather than clipping off the whole fin, left a more serviceable fin. Since the scar of the cut and the different appearance of the regenerated tissue were still quite discernable in October 1953 it was an adequate mark. (It would not have been, however, if the fish had been marked for sportsmen to recognize.) In 1952 and 1953 fish were tagged with single hole plastic tags (Fry 1947) sewn about the preopercle bone with 6 lb. test monofilament nylon using a curved needle and surgical needle holder (Fig. 2). Recaptures in the fall of 1952 made it apparent that very few fish were losing tags. In 1952, only one fish out of the 76 recaptured during that period had lost a tag and in

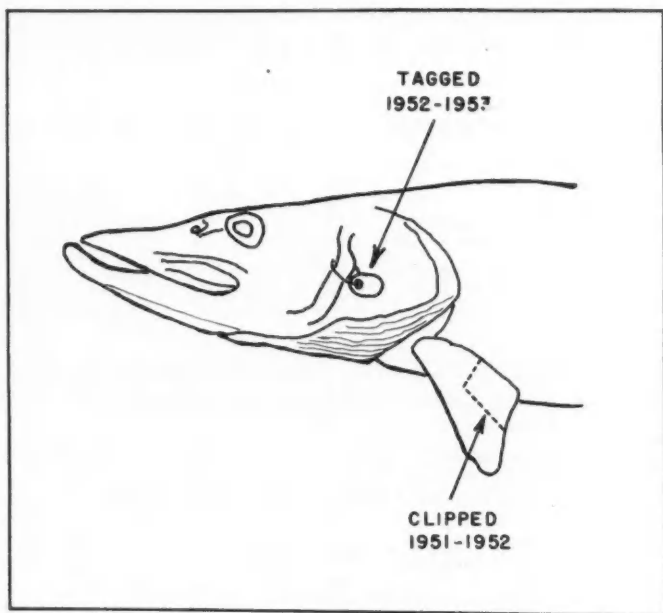


FIG. 2.—Markings used, 1951-1953.

1953 only three out of 132 recaptures had lost a tag. When the surface temperature of the water rose above 70° F. (late June) maskinonge were tagged while under approximately eight inches of water in a galvanized tank.

In the five marking periods from May 1951 to October 1953, a total of 770 maskinonge were marked by means of fin clipping, tagging, or both. Table I shows the record of captures in each netting period.

The age of each fish captured was determined by the scale method. Impressions of the scales were prepared, by means of a roller, on cellulose acetate slides as described by Arnold (1951).

TABLE I.—Summary of fish caught, marked and recaptured 1951–1953.

Year		Total fish handled	Releases	Recaptures
1951		181	164	17
1952	Summer	176	124	52
	Fall	174	150	24
1953	Summer	300	218	82
	Fall	164	114	50
Totals		995	770	225

SIZE COMPOSITION

RESULTS

The average size and the size range for each netting period is given in Table II. The overall size range was from 23 cm. to 91 cm. (S.L.) and the overall mean 53.0 cm. The size distribution of the summer and fall catches in 1952 and 1953 (not shown) differed significantly. In 1952 the modal size was larger in the summer than in the fall. In 1953 the reverse was true corresponding with the observation that larger fish moved greater distances in the fall than the summer.

TABLE II.—Average size (standard length) and size range of fish caught in each netting period 1951–1953.

	1951	1952			1953		
	Summer	Summer	Fall	Year's total	Summer	Fall	Year's total
Average size, cm.	51.8	53.8	50.9	51.4	49.2	57.8	52.2
Size range, cm.	25–87	23–81	37–71	23–81	25–72	43–91	25–91

AGE COMPOSITION

Table III gives the age composition of each year's catch of maskinonge. Age, as given, is the number of annuli (years growth) completed, so that age-group I

TABLE III.—Age composition of maskinonge netted in Nogies Creek 1951–1953.

Age:	I	II	III	IV	V	VI	VII	VIII	IX	Total
1951	6	67	70	29	3	3	0	1	2	181
1952	0	75	136	96	38	4	1	0	0	350
1953	3	107	191	115	33	11	3	0	1	464
Total	9	249	397	240	74	18	4	1	3	995

fish are in their second year of growth. With the gear used, I-, II-, and perhaps even III-year-old fish are not caught in proportion to their abundance.

MORTALITY RATE

Figure 3 shows the catch curves (Ricker 1948) of maskinonge in the years 1951–1953. The left, or ascending limb is not shown. In each year's data the right limb of the catch curve for maskinonge in Nogies Creek describes a mortality rate of approximately 70% per year after the third year.

Variations in success of individual year classes tend to deform the curve, e.g. ages seven to nine in the 1951 line. A mortality rate independent of this variability can be estimated from a catch curve of a stable group of marked fish, i.e., if the number of III-year-old fish marked in 1951 is followed through the number of marked, IV-year-olds recaptured in 1952 and the number of marked,

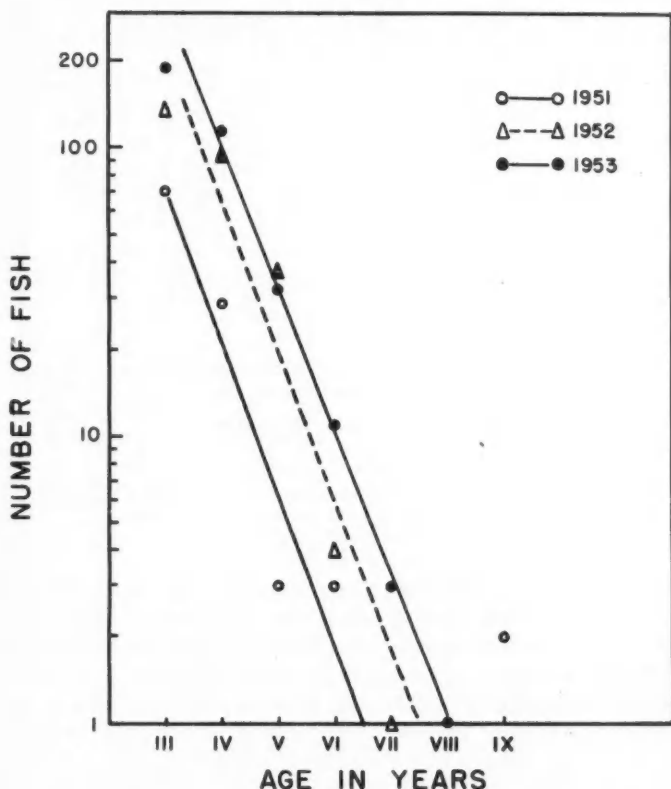


FIG. 3.—Catch curves of maskinonge in Nogies Creek 1951–1953. Only the right or descending limb of the curve is shown.

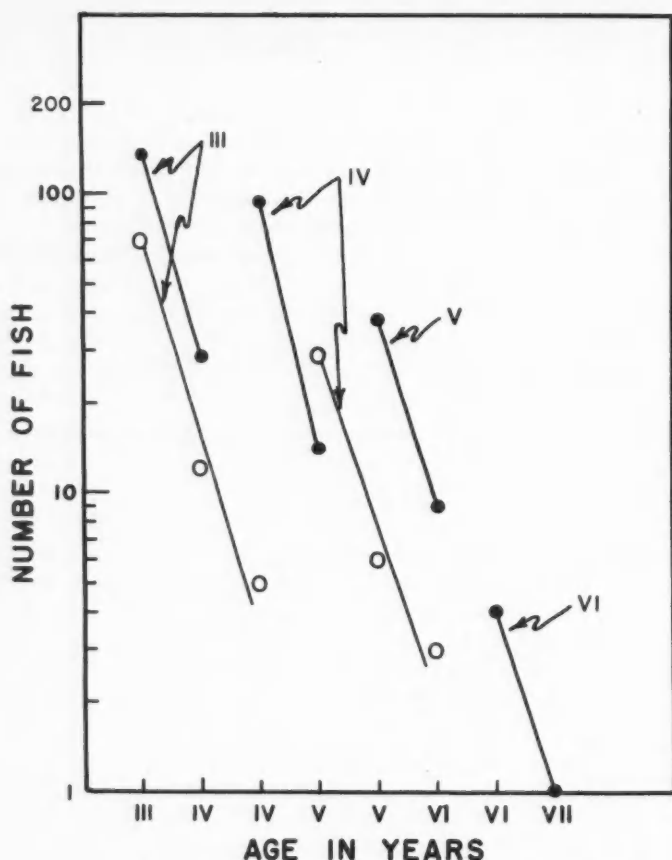


FIG. 4.—Catch curves for maskinonge marked and recaptured. *Open circles* are fish marked in 1951 and recaptured in 1952 and 1953. *Closed circles* are fish marked in 1952 and recaptured in 1953.

V-year-olds recaptured in 1953. If the resulting lines are similar to those for the total catch curves, then we can place more confidence in the slope of the catch curves as indicators of mortality rate. Figure 4 in this way substantiates the 70% mortality rate estimated from the catch curves of Figure 3.

The small numbers of older fish taken was apparently not due to selectivity of the gear. In test angling over the whole area of the sanctuary, no fish older than six years of age were taken, but otherwise the age frequency conformed to that of the net catches. Angling was done in areas in which nets could not be set, due to depth, and which might have sheltered older fish had they been present.

In contrast to the Nogies Creek catch curves are the curves based on other lakes in the area (Fig. 5). These curves show a mortality rate of approximately 40% from age III onwards, or 30% less than that in Nogies Creek. They also show peaks in the numbers taken at ages greater than III.

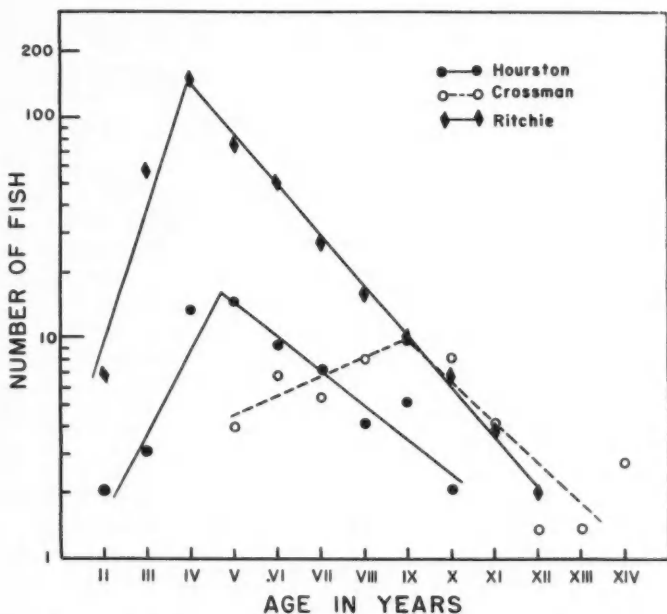


FIG. 5.—Catch curves for maskinonge in other lakes in the area. Hourston's data are for his central region which includes Pigeon Lake. The author's data are the 1952, 1953 average from creel census for Pigeon and Sturgeon Lakes. Ritchie's 1953 data are trap net catches for Lake Scugog.

RATE OF GROWTH

Figure 6 shows the age-length relationship of maskinonge in Nogies Creek. It was said locally that at one time the maskinonge of Nogies Creek exhibited a retarded rate of growth, and that a great many of them were "snake-like", that is, with large heads and very slender long bodies. However, the rate of growth compares favourably with that given by Hourston (1952) for what he terms the central region of the distribution of this species, i.e. central southern Ontario between Lake Ontario and Georgian Bay, which includes the Kawartha lakes and Nogies Creek. The growth rate compares well, also, with that given by Schloemer (1936), as an average for five Wisconsin lakes (Fig. 6).

As Hourston indicates, there is great variation exhibited in the age-length relationship of the maskinonge of this region. This is shown by an average spread of 15 cm. about the mean size for any year-class calculated for the Nogies Creek

fish. However, there is a definite curvilinear relationship between standard length and age, the length increment per year becoming smaller with increasing age. The annual increments in size for Nogies Creek are plotted with the age-length curve in Figure 6. It shows the increment to be very high between the first and second year with a rapid decline to the fourth year. From the fourth to the eighth year it is fairly uniform.

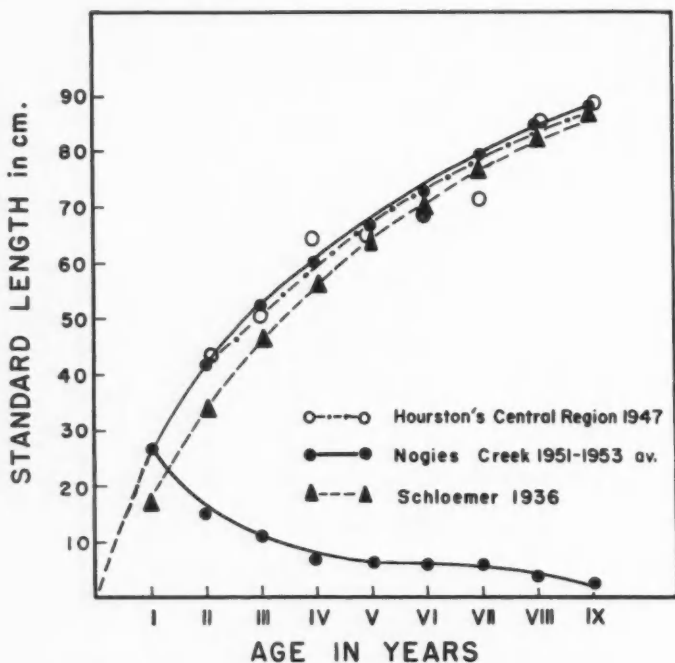


FIG. 6.—Comparison of age-length relationship of maskinonge in various waters. The annual increments in length are given for Nogies Creek only.

Schloemer gives the average standard length at the end of the first year of life as 17.8 cm. (7.0 in.) S.L. for the Wisconsin maskinonge. Although he gives this as the size at the *end of the first year* of growth, he interprets age in the same manner as the author, that is, age-group I fish are in their second year of growth. The Nogies Creek maskinonge are 26.3 cm. (10½ in.) at one year and therefore exhibit a greater rate of growth in the first year than those in Wisconsin.

A possible explanation for this is found in Eddy and Carlander (1942). They describe a "period of variation" which, they say, indicates that in several species of fish, the growth is most responsive to the environment during the early years of life. After this period the growth rate is more nearly the same in all environ-

ments and lakes. Nogies Creek is small and has an extreme abundance of four to six inch forage minnows, which would be utilized by maskinonge in their first year. This may explain the greater rate of growth in the first year in Nogies Creek compared to that of fish in larger lakes with a relatively smaller amount of forage minnows in relation to the area.

This growth rate of young fish in Nogies Creek under natural conditions is approximately equal to that quoted by Elson (1941), for Elson states that the rate of growth in the first summer for maskinonge fed on minnows in a closed area cleared of predators, is approximately 10 inches (8 in. - 11½ in.). This is for a six month period, and for fish that have completed one annulus, 13.1 inches.

MOVEMENTS

The number of fish tagged and released in 1952 and 1953, from which the movements were determined, are shown in Table IV.

The number of maskinonge which were caught more than twice gives a good check on the wanderings of these fish. Sixteen fish were captured 3 times and other individuals as many as 10 times.

On the whole the maskinonge of Nogies Creek showed great variability in movements. Several fish were caught several times during the summers of 1952 and 1953 at the site of marking. Very few fish were caught in the summer at a site other than that at which they were marked. In fact one maskinonge was captured ten times in the two summers at netting sites 6 and 7 (Fig. 1) which are separated by only twenty feet. In contrast to this, the greatest distance travelled by a single fish in summer was 6,600 feet downstream and then 1,810 feet upstream between May 12 and June 6, 1952. Circumstantial evidence suggests there was little movement in summer.

TABLE IV.—Maskinonge tagged and recaptured 1952-1953.

		Recaptured in 1952		Recaptured in 1953	
		No.	% of No. tagged	No.	% of No. tagged
No. tagged in 1952	274	44	16.05	47	17.15
No. tagged in 1953	332			54	16.26

The distance travelled in feet in relation to the time out in days and to the season between recaptures varies also, ranging from no distance for 484 days out (1952) to 1050 feet travelled for 1 day out (1953). Data (not included) shows a greater amount of travel for greater numbers of days out, but the relation here seems to be more one of distance travelled to season.

Recapture data indicated that a greater number of fish were travelling in the fall than in the summer. Fish tagged and released in the summer and then recaptured in the fall show movement during that interval. All fish tagged in the

fall and recaptured that fall, show movement. However, fish tagged in the summer, released and recaptured that same summer, show little movement. Of the 52 recaptured maskinonge exhibiting no movement, 24 were caught during the summer they were tagged. Of the remainder of the fish exhibiting no movement 14 were tagged in the summer of 1952 and recaptured in the summer of 1953. These fish either did not move during that period of time, from summer to summer, or if they did, they had returned to the same spot by the second summer. Only one case appeared of a fish tagged and released in the fall and recaptured in the following summer. This fish had moved, and might have moved during the fall.

The distance travelled in relation to age and size showed a considerable degree of variation. However, the figures did suggest an increase in distance travelled with age at least between age-groups III and VII. The data also suggested a peak in distance travelled at the 35-45 cm. size range, a drop in the next two size ranges and another peak at the 65-75 cm. size range.

Of all the cases of recaptured maskinonge showing distance travelled, two stand out. A V-year-old fish 63 cm. in length, was tagged on July 1, 1952. It was recaptured a year later twenty feet away from the tagging site. However, on October 2, 1953, it was recaptured and since its last capture it had travelled 1320 feet downstream. Seven days later it was recaptured two miles upstream.

A IV-year-old fish, one of the maskinonge released into Pigeon Lake from Nogies Creek in October 1952, was caught by an angler on July 7, 1953 in Chemong Lake. It had travelled a distance of 25 miles in that time. In contrast to this is the larger number of fish which were taken by anglers, on or about this same day, in the same bay of Pigeon Lake, into which all the fish had been released in the preceding October.

POPULATION NUMBERS

Table I above shows the number of maskinonge caught, marked and recaptured in each of the netting periods from 1951 to 1953. It is on these figures that the estimation of the population of maskinonge in the area studied is based. The number of fish marked and the number of recaptures in each netting period is small, so the estimate of the population will be only approximate.

After seeking the advice of Dr. D. B. DeLury, it was decided that the Schumacher method with DeLury's revised treatment of confidence limits would yield the best results considering the small numbers to be used. It was felt the numbers were not large enough to warrant the more complicated statistical treatment of some population estimates. Although the Schumacher estimate will be used for the final population estimate, a Schnabel type estimate and a Petersen type estimate were made to compare results from the various methods.

Schnabel estimates were made on the day to day catch data of the summer netting periods of 1951-1953, according to the method outlined by Schaefer (1951). Schumacher estimates with 95% confidence limits were made for these data by the method outlined by DeLury (personal communication) as shown:

when:

n_t = total number in t^{th} sample

x_t = number of tagged recaptures in t^{th} sample

T_t = number of tagged individuals in population just before t^{th} sample is taken

k = number of samples

N = size of population

\hat{N} = estimate of N

Then the formula is:

$$\hat{N} = \frac{\sum n_t T_t^2}{\sum x_t T_t}$$

$$(k-1)s^2 = \sum \left[\frac{x_t^2}{n_t} \right] - \frac{(\sum x_t T_t)^2}{\sum n_t T_t^2}$$

And DeLury's revised 95% confidence limits for \hat{N} are given by:

$$\frac{\sum n_t T_t^2}{\sum x_t T_t \pm 2s \sqrt{\sum n_t T_t^2}}$$

Petersen estimates were made for 1952 and 1953, using the fall netting periods as sampling periods for tags put on in the summer of the respective years. Table V shows the population estimates by these various methods.

The estimates seem uniform except for the 1952 figures for Schnabel and Schumacher methods. The Schnabel and Schumacher methods are in each case probably low due to the fact that they depend on the summer period and are based on the fish vulnerable to the nets during that time only. The Petersen estimates are probably high in each case since they are based on a relatively small number of recaptures of summer marks in the fall netting period.

The Schumacher method sets an estimate of the maskinonge, in that part of the sanctuary studied, somewhere between 769 and 1,122 in July, 1953.

Since these figures represent the population of only that part of Nogies Creek studied, that is from Watson's Bridge to the lower boundary of the sanctuary (see Fig. 1), then the population of maskinonge in the whole sanctuary must be larger.

TABLE V.—Population estimates by various methods. (95% limits of confidence are included for the Schumacher estimates only).

	Schnabel	Schumacher	Petersen
1951	886	998 (764-1101)	—
1952	608	657 (508-929)	981
1953	932	912 (769-1122)	966

DISCUSSION

A sanctuary which does not allow free access of fish to water open to angling, does not serve the purpose for which it is established. Proper utilization of the fish in such a sanctuary must involve moving fish to open water.

The data presented indicate an annual mortality rate of 70% in fish of III years of age and older in Nogies Creek. Two possible explanations of this are: extensive winter kill in shallow Big Marsh, or a lack of forage fish of sufficient size for maskinonge over III years of age. There are great quantities of minnows suitable as food for year-old maskinonge and a large population of sunfish (9855 caught 1951-1953) possibly utilized by II- to IV-year-old fish. However, there are not large numbers of medium to large size perch, suckers and bullheads for maskinonge over IV years of age. In 1951-53 only 829 individuals of these species combined were taken. This latter factor may have led to cannibalism of large maskinonge on smaller maskinonge. Catches subsequent to those reported here show that large maskinonge (over 30 inches) returned to the sanctuary in the fall netting periods, reappear in the catch in numbers out of proportion with their supposed ratio in the population. This supports the hypothesis of cannibalism as a result of insufficient forage.

Since this annual mortality rate is higher than the 40% for lakes in the area which are open to angling (Hourston 1952, Ritchie 1953), then as many maskinonge as possible, especially the III-year-old and older fish, should be moved from Nogies Creek Sanctuary to open lakes. These fish would enter the sport fishery in one or two years and help support it sooner than hatchery fish. Maskinonge of over 30 inches in length and presumably of spawning age, which appeared to be succeeding, could be left as breeding stock. A decrease in the number of older fish might leave sufficient forage to adequately support the breeding population.

A second contribution to the sport fishery of a sanctuary of this type could be its function as a "nursery" for hatchery reared fish. Maskinonge in Nogies Creek show a growth rate of 26.3 cm. (S.L.) in the first year. This is equal to the growth rate for larger lakes in the area (Hourston 1952) and comparable to artificially fed maskinonge held in a lake (Elson 1941). It might be advantageous to move hatchery fish to the sanctuary for one or two years before releasing them in larger lakes. The rapid growth they might achieve feeding on the abundant minnows might insure a greater success in the stocking of the larger lakes. Also these fish could be marked before release and perhaps provide some information on the contribution of hatchery fish to the anglers' catch.

The value of this second use of the sanctuary is limited by the degree to which the 70% annual mortality affects fish less than III years of age. From the data presented it is impossible to say whether the mortality of young fish is greater or less than that for fish III years old and older. However, a decrease in the number of older fish could possibly lead to sufficient forage to support those present. This could alleviate cannibalism if present and allow a greater number of young fish to utilize the abundant food available for maskinonge of smaller sizes.

The application of the first and possibly both of these procedures to the Nogies Creek Sanctuary will lead to worthwhile utilization of a stock of valuable game fish, which previous to 1952 were unavailable to anglers. Nogies Creek has been serving as a museum rather than a sanctuary, and unless the fish in it are utilized it will not be serving any useful purpose.

SUMMARY

1. The population of maskinonge (*Esox masquinongy* Mitchill) of Nogies Creek, Ontario was studied by means of a netting and marking program, carried out in the years 1951 to 1953 inclusive. In five netting periods during this time a total of 995 maskinonge were caught. Of these, 770 were caught only once (releases) and 225 were recaptured at least once.

2. The maskinonge were marked by fin clipping in 1951, fin clipping and tagging in 1952, and tagging in 1953. The tag used was the Ontario Department of Lands and Forests single hole plastic tag. In all cases the tag was sewn about the preopercle bone with monofilament nylon.

3. Tag losses of maskinonge were calculated to be 1.3% in 1952 and 2.3% in 1953. These figures are based on tags missing in October of the year they were put on.

4. The overall average size of maskinonge caught from 1951 to 1953 was 53.0 cm. S.L.

5. Maskinonge of age-groups II, III and IV predominated in the catch. The mesh size of the nets was such that only a small number of I-year-old and II-year-old fish were caught. The small number of maskinonge over III years of age was apparently due to a 70% annual mortality rate. This 70% mortality rate in Nogies Creek is higher than that of other lakes in the area. Pigeon, Sturgeon and Scugog lakes show an annual mortality rate of approximately 40%.

6. The rate of growth of maskinonge in Nogies Creek, in the first year is 26.3 cm. (S.L.). This is only slightly greater than the 25.5 cm. attained for maskinonge in other lakes in the area. However, it is 8.5 cm. greater than the 17.8 calculated by Schloemer as an average for five Wisconsin lakes. The growth rate during the first year in Nogies Creek compares well with that of maskinonge reared in a closed area and fed with minnows. After the second year the growth parallels that found in other Ontario and Wisconsin lakes.

7. There was little movement of maskinonge in summer and what movement there was was mainly upstream. In the fall there was far more movement, and this was mainly in a downstream direction.

8. An estimate, based on the recaptures of marked fish and calculated by the Schumacher method, set the population of maskinonge, in that part of the sanctuary studied, somewhere between 769 and 1,122 in July, 1953.

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their directors and staff and the support of the Fish and Wildlife Division of the Ontario Department of Lands and Forests. I wish to express my appreciation of the guidance and advice given by Dr. F. E. J. Fry and others of the Zoology Department of the University of Toronto during this investigation and the writing of the M.A. thesis from which this material is derived. To Dr. P. A. Larkin I extend thanks for his constructive advice on the final preparation of this paper.

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The Choice and Solution of Mathematical Models for Predicting and Maximizing the Yield of a Fishery^{1,2}

KENNETH E. F. WATT³

Ontario Department of Lands and Forests

ABSTRACT

The great expense of modern fisheries research programs necessitates, prior to data collection, careful consideration of the mathematical model to be used in analysis. The simplest type of model requires little information, but has poor predictive reliability. Progressively more complex models have higher information output, in the form of predictive reliability and insight into dynamics of the exploited population, but require higher information input, not only as amount of data, but array of types of data. The general form of the most complex type of model is derived by consideration of available information on the dynamics of fish populations. The specific form of the component terms and the values of the parameters must be derived in each instance through a combination of deduction and joint regression analysis. To solve the models, catch-effort data must be weighted to avoid gross errors, all readable scales must be aged, regardless of difficulty in interpretation, and various modifications of the theory and practice of tag-recapture programs are necessary. Schooling behaviour and regenerative scale centers influence necessary minimum size of scale sample.

INTRODUCTION

THE modern fisheries research program is expensive. If we are to gain sufficient insight into the dynamics of a population to predict its behaviour under exploitation, large bodies of data must be collected over a several-year period, great numbers of scales or bony parts must be read for age determinations, and an expensive, laborious analysis must be undertaken. Considering costs of labor, maintenance, equipment, transportation, buildings and purchase or rental of electronic computing apparatus, it is difficult to see how any worthwhile, and economically applicable study of a fish resource can cost less than a few score thousands of dollars. There are many fishery research units in the world with an annual budget several times this much.

A fishery research program which lacks at the outset a carefully conceived plan, but collects data first and attempts interpretation afterwards, can be very wasteful. Funds, time and energy can be dissipated, not only by collecting insufficient data, but also by collecting superfluous data. Furthermore, as a result of inadequate preliminary planning, a research program may be based on an utterly incorrect approach to the problem at hand, and may collect the wrong type of data altogether. For example, it will become apparent through the course

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³Author's address: Ontario Department of Lands and Forests, Southern Research Station, Maple, Ontario.

of this paper that there are fisheries for which any tagging program at all is wasteful, because the problems under consideration can satisfactorily, and most economically, be solved by a form of catch-effort analysis.

Acknowledging the need for a good research plan, let us begin with consideration of its essential elements. The plan should dictate the types of data to be collected, the number of each type to be collected, and the design of the scheme for collection. However, this statement of the nature of the plan is superficial, since it omits the most important element: choice of the mathematical model to be used in analysis of the data. The model is of primary importance, because the choice of model to be used determines the type and amount of data we need, and the design of the data-collection procedure. I believe the whole matter of models in fisheries research is sufficiently important to justify this paper which focuses attention on their choice and solution.

There are at present four basic types of models which are actually used or could be used to predict the yield of a fishery, or to show how to maximize the yield. The plan of this paper is as follows. Each of the models will be assessed with regard to what it produces in exchange for the types and amounts of information that must be fed into it for its solution. Decisions as to the possibility of meeting input requirements continuously over a series of years, the nature of the resource, and the level of predictive reliability desired are the factors which should determine the choice of model. Once the model has been chosen, various field problems arise in obtaining data for its solution. Circumventing these problems through modification of program design will constitute the topic of the second half of the paper.

The mathematical development of models already published will not be presented here; this paper is not intended as an exhaustive review of existing literature. However, in order to present a thorough discussion of the application of various mathematical models, it is necessary that we consider the assumptions used in their development.

TYPES OF MATHEMATICAL MODELS OF USE IN PREDICTION

For the purposes of this paper, I shall assume that the following are the two major aims of research on fish populations.

1. Predicting the catch in subsequent years.
2. Predicting how to maximize the catch in subsequent years.

The models are classified into four categories on the basis of the type of information they require. In this section of the paper, I shall discuss each of the four types of model in turn, with respect to the following items.

1. Information needed.
2. Assumptions on which the mathematical development is based.
3. Predictive reliability.
4. Advantages and disadvantages.

The more complicated models may be needed for the following two reasons. First, annual variations of factors governing productivity of the population under study may introduce year-to-year fluctuations in productivity that cannot be

handled by the simpler types of models. Second, it may be necessary for purpose of management of the resource to predict productivity with a high degree of precision.

The aim of the following discussion on types of models is to show the extent to which increasing data requirements of the more complex models are justified by their ability to meet the above two needs. In other words, for each of the models, we shall weigh its information output against its information input. This should enable the researcher to see what type of model he will require to obtain the predictive reliability and corollary information he decides he needs. His choice of model then in turn determines the data he requires.

TYPE I MODEL

The simplest type of model of exploited fish populations is characterized by requiring no data on the age structure of either the landed catch or the stock left in the water. Efforts along these lines are traceable back to Russell (1931), who noted that where:

- P_1 represents the weight of the catchable stock at the beginning of a year,
- P_2 represents the weight of the catchable stock at the end of that year,
- A is the amount by which recruitment increases the weight of the catchable stock during the year,
- G is the increase in weight of the catchable stock due to growth during the year,
- M is the decrease in weight of the stock lost to natural mortality during the year, and
- C is the weight of the annual catch,

$$P_2 = P_1 + A + G - M - C \quad (1)$$

Other men utilizing the same basic approach as Russell, but incorporating theory associated with the logistic curve into their thinking, were Baerends (1947), Bückmann (1938), Graham (1935, 1938, 1939, 1944) and Hjort, Jahn and Ottestad (1933).

A recent modification of this technique was presented by Schaefer (1954a, 1954b), who notes that where:

ΔP denotes $P_2 - P_1$,

$\bar{f}(P)$ denotes the annual natural rate of increase corresponding to the mean stock during the year,

F_t is the total number of units of effort during the year,

KF_t is the instantaneous fishing mortality rate, and

\bar{P} is the mean population during the year,

(1) may be rewritten as:

$$\Delta P = (A + G - M) - C$$

which in turn is equivalent to:

$$\Delta P = \bar{f}(\bar{P}) - KF_t \bar{P} \quad (2)$$

Prediction, using this approach, assumes that a roughly parabolic relationship exists between $\bar{f}(\bar{P})$ and \bar{P} .

The only information needed to solve (2) is data on total catch, total effort, and the instantaneous fishing mortality rate. The last-mentioned datum is obtained by tagging.

A large number of assumptions are inherent in this model. \bar{P} is assumed to be the only factor causing variation in $\bar{f}(\bar{P})$, which is certainly not in agreement with the available evidence (see discussion of type IV model). The assumption that all elemental rate parameters of the population may be combined to produce a simple functional relationship between rate of increase and stock size does not take cognizance of modern work on competition, which shows that the population effects of different age groups within a species may be very different. (Fecundity, natality, tendency to disperse and intraspecific competition pressure exerted by an animal are probably all functions of its age for most species). Also, catch per unit effort is taken to be proportional to the population encountered by the fishery, and the instantaneous rate of fishing mortality is considered as proportional to the number of units of fishing effort.

As might be expected when so many assumptions are used in development of the model, its predictive reliability is not too good, as may be seen from figures 2 and 9 in Schaefer's (1954b) paper.

However, Schaefer filled a definite need when he proposed this simple, yet ingenious model. He was familiar with the more complex approach originating with Baranov (1918) and recently worked on by Beverton, Holt, Hulme, Jones and Parrish (see, for example, Beverton, 1953). However, as he says, "The introduction of variations of the elemental rates with population density into such a model presents a good many complexities, and the writer knows of no stock of sea fishes for which enough is known about these relationships to make possible any precise calculations" (Schaefer, 1954a).

The type I model is useful where it is difficult or impossible for technical or economic reasons to obtain sufficient data to use one of the following three types.

TYPE II MODEL

The second type of model requires only information on effort expended and the age structure of the catch. The notion basic to this approach is that from a knowledge of the catch per unit effort of a year-class last year, we can predict the catch of the same year class that will be caught this year by a predetermined amount of effort. Farran (1930), Lea (1930) and Thompson (1930) presented ideas which reappear in the two modern variations of this approach, those of Fry (1949) and Royce and Schuck (1954).

This approach may be formulated mathematically as the regression equation:

$$C_N = a + bC_{N-1} + cE_{N-1} + dE_N \quad (3)$$

where:

C_N represents the number (or weight) of the year-class caught in year N ,

C_{N-1} represents the number (or weight) of the year-class caught in year $N - 1$,

E_N represents the total effort expended (against all year-classes) in year N , and

E_{N-1} represents the total effort expended in year $N - 1$.

a , b , c and d are constants determined through regression analysis of the catch statistics for a series of years.

Probably the worst assumption made when using this approach is that the size of the first year-class to enter the fishery each year will be constant. This assumption must be made, because of the way in which the model is formulated (see equation 3). Apart from this weakness, the method is liable to the usual difficulties associated with catch-effort studies. The number of fish caught per unit effort may fluctuate as a result of hydrographic factors even when the stock in the water remains constant (Jensen, 1939).

The predictive reliability of this type of model may be very high where it is applied in appropriate situations. Royce and Schuck found that 83 per cent of the variability in catch from year to year was accounted for by using their regression equations for Georges Bank haddock. Predicted catches for 1951 and 1952 were 102 and 101 per cent of the actual landings, respectively.

In discussion of the advantages and disadvantages of this approach, it is worthwhile to devote some attention to determination of the situations in which it is appropriate. A major weakness of the method is its inability to make predictions about the strength of the youngest year-class liable to exploitation in any year. Hence the model will work best where the effect on the fishery of variations in the incoming year-class is negligible, because many year-classes are fished, or where the environment is so stable that the size of the year-class entering the fishery is indeed almost constant from year to year.

A second weakness in the type II model is that it assumes the ratio of number of 8-year-olds in the water to the number of 7-year-olds the previous year is constant from year to year, and that the ratio of mean weight of 8-year-olds to that of 7-year-olds the previous year is constant from year to year. This assumption would not hold where the force of one or a number of environmental factors was fluctuating markedly from year to year.

A third weakness in the type II model is that it doesn't show how to maximize recruitment or growth, since it does not deal with conditions in the water which govern survival, natality or growth of a year class prior to the time at which it enters the fishery.

The big advantage of the method is that when it is applied to fish populations that do live under fairly uniform environmental conditions, and in which year-classes are in the fishery for several years, it gives a high predictive reliability in exchange for information obtainable cheaply and readily. All the expense and labor of obtaining information about the stock left in the water through tagging and certain types of catch-effort studies is avoided.

TYPE III MODEL

This type of model requires information on the age structure of the catch and the size of fish at various ages. In addition, it requires data on instantaneous natural and fishing mortality coefficients and recruitment, which necessitates a tagging program. The applicability of the type III approach has probably been explored more thoroughly than that of any of the four types of models. The initial work on this type of model was done by Baranov (1918), but the whole approach, or aspects of it have been discussed and modified by W. F. Thompson and Bell (1934), Ricker (1940, 1944, 1945), Hulme, Beverton and Holt (1947), Yoshihara (1952), Beverton (1953, 1954), Parrish and Jones (1953) and Beverton and Holt (in press).

The most recent version of this theory in print (Beverton, 1953) has the following form:

$$Y_w = FRW_{\infty} e^{-M(t_p' - t_p)} \sum_{n=0}^3 \frac{\Omega_n e^{-nK(t_p' - t_0)}}{F + M + nK} [1 - e^{-(F+M+nK)(t_{\lambda} - t_p')}]$$

where: $\Omega_0 = +1$, $\Omega_1 = -3$, $\Omega_2 = +3$, $\Omega_3 = -1$

Y_w is the total yield in weight obtained by the fishery from a year class throughout its life

F is the instantaneous fishing mortality coefficient

R is the number of fish in the year class (brood) at the time it is first recruited into the area where fishing is in progress

W_{∞} , K and t_0 are physiological constants describing the form of the growth function

M is the instantaneous natural mortality coefficient

t_p is the age at which the brood is first recruited to the area where fishing is in progress

t_p' is the age at which surviving members of the brood are first liable to capture by the fishing gear, and

t_{λ} is the last age to which members of the brood are likely to survive.

The form of this model currently in print assumes a steady state fishery, that is, recruitment, growth and natural mortality are constant from year to year. However, the model could be modified to enable it to handle temporal changes of elemental parameters of the population.

It would be difficult and unfair to attempt an evaluation of the predictive reliability and advantages and disadvantages of this model at the present time, since the papers which have appeared on it to date should probably be accepted only as progress reports on a still-continuing program. Presumably Beverton at Lowestoft, Holt in Rome, Jones at Aberdeen, and others are all actively exploring the potentialities of this type of approach, and a final evaluation should not be made until their results are in print.

The big advantage of the type III approach over the two previously mentioned is that it gives more insight into the dynamics of the exploited resource. The evaluation of the final form of this model will depend on its ability to cope with annual fluctuations of hydrographic factors, size of spawning stock, interspecific competition, and all the other factors which can govern natality, survival and growth.

TYPE IV MODEL

Finally, I should like to discuss a type of model which has not yet been applied to a fishery, but which has, potentially, the highest predictive reliability that it is possible for a model to have.

The information needed for this type of model to have maximum predictive reliability is the age distribution of the stock in the water, the growth rate for each year class, and data on hydrographic factors, interspecific competition, pathogen population level, and any other factors which can govern the productivity of the population in question.

This type of model does not assume a steady state fishery. It employs a mathematical rationale requiring an empirical program which will dictate the form of the model and the values of the parameters, and which will collect data on all factors which can conceivably affect the productivity of the population in question.

There are alternative procedures we could follow to arrive at the form of a fourth type of model. On one hand, we could use pure deduction, and derive a model in the same fashion as a mathematical theorem, starting with certain reasonable assumptions, and manipulating equations that followed from these to obtain the productivity equation. On the other hand, we could use a purely inductive attack. After examining all available evidence on the behaviour of exploited fish populations, we could proceed to formulate a general model which was based on empirical reality. After this we would derive the values for the parameters and the form of the component terms of the productivity equation from empirical study of each particular case.

For two reasons, I have decided to use an inductive procedure. First, experience showed the writer that elaborate deductive models which appeared logically sound did not in fact describe reality as observed in laboratory or nature. As a result, I believe that the form of a mathematical model for use in the analysis, prediction, and management of a natural phenomenon should be determined inductively, not deductively. This does not mean that I lack faith in man's logical ability. Rather, it indicates that I question the ability of his imagination to conceive of all the independent variables which can participate in government of a complex system, and the incredibly subtle ways in which the variables can interact. Hence I believe that quantitative empirical findings constitute the only reliable route to insight, where phenomena are complex. Second, the model to be presented here, while simple in its general form, can be dismayingly complex when the forms of all the component terms have been determined, and the values of the parameters filled in. A completed equation

obtained using a very simple type IV model for a laboratory population (Watt, 1955) is probably elementary compared to the corresponding equation that would be obtained from many natural populations. Therefore, an examination of the available information on the dynamics of exploited fish populations will be undertaken herewith, to defend the notion that there is indeed a legitimate justification for equations of such complexity.

The discussion will be organized as follows. Each desideratum for a realistic model will be stated in turn, and after each will be marshalled empirical evidence indicating why a model must be formulated in accord with this desideratum in order to be realistic.

The first desideratum is that the model consider separately, growth of a year class on one hand, and numerical strength (the resultant of natality and survival) on the other. Year class strength and first year growth were not correlated for rock bass (Hile, 1941) or yellow perch (Pycha and Smith, 1955).

Second, there are two different types of maximization problems that a model must handle if it is to be realistic and of maximum use in predicting and showing how to maximize catches. First, the model must show how to most efficiently exploit the growth potential of the stock already recruited. If a year-class is fished too early, we lose the biomass yield that would have resulted from growth; fishing the brood too late wastes too much biomass to natural mortality. Second, great annual variations in year-class biomass recruitment occur. A model which considers only the first of these problems can never show how to obtain the absolute maximum sustained yield, since it ignores many of the factors which govern the size of the yield. Furthermore, some of the factors which it ignores, such as size of spawning stock and intra- and interspecies competition in the years prior to recruitment, are susceptible to economically-rewarding manipulation by man.

A third requirement of a realistic model is that it be flexible enough in form to handle all the factors which are known to be able to control growth, natality and survival in fish populations (Hile, 1954a). It seems well worth while to introduce here a fairly thorough discussion of the types of factors which can govern the dynamics of fish populations, since the great array of these factors, more than any other point, argues for a quite complex model.

The factors governing growth will be treated first. Then the factors controlling natality and survival will be considered together, because it is sometimes difficult to determine precisely how a certain factor has operated to produce great annual variations in year class recruitment.

In the classification of environmental factors I am following Andrewartha and Birch (1954). They reason that the following four categories of factors constitute the components of an individual animal's environment:

1. weather
2. food
3. other animals of the same kind, other animals of other kinds, and pathogens
4. a place in which to live.

FACTORS GOVERNING GROWTH

Many different workers have shown that weather affects rate of growth. Hile (1941) correlated growth of rock bass in Northern Wisconsin with average air temperatures in June and September and precipitation in June. Van Oosten and Hile (1949) showed that low turbidity in combination with heavy precipitation was beneficial for the growth of lake whitefish. It was impossible to separate the effects of the two independent variables, since they were highly correlated with each other. Anderson (1951) and Svetovidov (1952) have noted that growth of herring is dependent on ocean temperature. In our own research, we have noted that width of annuli of smallmouth black bass is correlated with the sum of the July to October heat experience in the years in which the annuli were formed.

Annual growth fluctuations may be correlated with changes in type (Rae, 1939) or amount of food (Langford and Martin, 1940). Since the food is determined by plankton abundance, it may be possible to express annual variations in growth rate directly as a function of plankton density (Breder and Nigrelli, 1936; Smith and Swingle, 1939). Plankton depends on chemicals in the water, so it should be possible to predict changes in fish growth as a function of changes in content of certain chemicals in the water. Bennett (1948) reports an odd case in which reduced growth was apparently due to reduction in the available food supply, caused by spread of a pond weed.

Other animals and pathogens affect growth rate of fish. Other animals of the same species can decrease growth rate, apparently, through competition for food, since thinning stock results in increased growth rates (Anderson, 1938, 1951; Beckman, 1941, 1943; Bennett, 1944; Elster, 1938; Hile, 1936; Molander, 1938; Ricker, 1937; Schneberger, 1935; Swingle and Smith, 1942). However Hjort (1932), arguing from Jensen's data on plaice, stresses that great changes in stock density need not cause changes in growth rate. Other animals of other species can decrease growth rate: Hile and Deason (1935) suggested that crowding by lake herring impeded growth of whitefish through competition for food or a "space factor" effect. Predation may increase growth rate by thinning out the prey. Bennett (1948) found that bass reduced a brood of bluegills to the point that those that escaped capture made excellent growth. Other species may increase growth by increasing available food (Larkin and Smith, 1954). Sometimes parasitism is the principal factor governing growth of a fish population (Reighard, 1929).

A decrease in the number of places in which to live may occur in two ways. First, the number of inhabitable niches may decrease for some reason, but second, more commonly, the amount of space per individual may decrease due to an increase in population density. There is reason to believe that crowding alone may cause decreased growth rate even where there is an excess of food present. Rate of stream flow can govern growth by affecting accessibility of most favourable places in which to live (Larkin, 1954). Hile (1936) recognized that a "space factor" may have accounted in part for differences in growth rate between four

populations of ciscoes. Moore (1941) showed that an excess of available food supply does not necessarily lead to increased consumption. Evidence in support of a "space factor" effect was presented by Willer (1929) and Johnson and Hasler (1954) but other evidence by Nikolsky and Kukushkin (1943) suggested that it only operates for some species. It is surprising, in view of the importance of a space factor if it does indeed exist, that so little work has been devoted to its study. This would lend itself very well to laboratory study, in which the amount of food and the population density of the consuming species were the two variables in an experimental design.

FACTORS GOVERNING NATALITY AND SURVIVAL

Dependence of strong year-classes on high temperatures during certain periods in the year of spawning has been found for blue pike (Doan, 1942), anchovies (Fowler, 1890), smallmouth black bass (Fry and Watt, 1955), pike-perch (Havinga, 1948), rock bass (Hile, 1941), and cod (Poulsen, 1930). The fish on which most work has been done in relating year-class strength to weather conditions in the year of spawning is the herring. Carruthers and Hodgson (1937) induced that year class production of herrings was increased by increasing temperature, increased rate of water flow, and increased barometric pressure gradient controlling movement of warm water masses into the spawning area. Rounsefell (1930) and Anderson (1951) also concluded that strong year classes of herring were dependent on warm water in the year of spawning. However, Anderson (1930) states, "During the autumn of 1925, the temperature of the water in the upper layers in the middle of the Baltic was unusually high, about 2° above normal. It has appeared that the spawning of that autumn did not bring forth a good year class". Svetovidov (1952), after reviewing the literature, concludes, "... generations resulting from years having high ocean temperatures have small numbers, fast growth, and early maturity. The generations from cold years are more abundant, smaller in size and reach their maturity later than the former ones". Tester (1951) has also found that "colder springs and summers result in year classes of greater abundance". The apparent discrepancy between the two groups of reports may be resolved in either of two ways. First, if a fish species is living in very cold water, years of high temperatures may bring forth strong year classes. If the species is living in warm or moderate water, cold years may result in strong year classes. Second, the discrepancy may be due to physiological differences in the different groups of herring under consideration. It should be noted here that very cold periods can kill warm water species (Gunter, 1941). Various writers have noted the importance of currents for the strength of a year-class. Currents may govern survival and natality in two ways. First, they determine the probability that tiny larvae reach and remain over the most suitable nursery grounds (Sette, 1943; Walford, 1938). Second, currents are important in moving warm water masses, and chemicals for plant growth with respect to the position of the fish (Carruthers and Hodgson, 1937; Svetovidov, 1952; Tait, 1952). The matter of the relationship of wind and water currents to fish survival is highly controversial. (Carruthers *et al.*, 1951, 1952; Graham, 1952; Gulland,

1952). Other components of weather that have been considered as important for year class strength are turbidity (Doan, 1942), salinity (Poulsen, 1930), precipitation (Hile, 1941; Sund, 1924) and CO_2 tension (Powers *et al.*, 1939).

Food may govern the survival of a year class (Sette, 1943), as well as its growth, and hence, so may chemicals such as phosphates (Cooper, 1948; Russell, 1939).

Other animals govern natality and survival of a year class in a great variety of ways. The size of the spawning stock determines numerical recruitment (Ricker, 1954; Jarvi, 1948), and the size of the spawning stock may in turn be deleteriously diminished by overfishing (Van Oosten, Hile and Jobes, 1946). It should be noted that overfishing is still a controversial issue (Graham, 1951; Huntsman, 1951) and very careful analysis is necessary to determine if overfishing has indeed occurred. Predator-prey relationships between different species are clearly demonstrated in many cases (Doan, 1942; Bennett, 1948); such relationships are important for survival of the prey species, as well as for growth of predator and prey species. Birds and other vertebrate predators may be important in regulating fish survival and growth (Huntsman, 1941; Trembley, 1948). Intraspecific competition and cannibalism can control survival (Ricker, 1950; Herrington, 1948). It will be very difficult to produce evidence showing that interspecific competition between fish populations has caused decreased survival in addition to decreased growth, but the evidence from other types of animals suggests that we must entertain interspecific competition as a logically possible cause of death (Park, 1948, 1954). On the basis of Park's experimental work, we should be prepared to find that interspecific competition is a very subtle and complex phenomenon, the outcome being the result of environmental and biotic factors, including pathogen density, and chance. Observations by Bennett (1944, 1952) suggest that interspecies competition does occur in fish populations and does operate through subtle and complex mechanisms. Pathogens can profoundly affect survival (Bardach, 1951).

The availability of places in which to live can affect natality and survival in a number of ways. The abundance of spawning sites can have a profound effect on fecundity of a population (Havinga, 1948; Reighard, 1943). The rate of stream flow in spawning streams can affect accessibility of spawning sites, and hence, the fecundity of the population (Jarvi, 1938, 1948; Larkin, 1954). A year-class of salmon never appeared, because while river discharge volume was high when salmon were ascending, it fell off after the fish were upstream and it was time for spawning. Evidently a combination of spawning failure and removal of ripe adults by poachers from the shallow water explains failure to spawn that year (Huntsman, 1953).

It is eminently clear from the preceding paragraphs that a great array of variables can play a role in fish population productivity. However, another point is an immediate corollary of this list. It will be noticed that more than one factor governs abundance of certain populations. For example, Poulsen (1930) concluded that the number of cod larvae in the months of April to May was correlated with the temperature of the bottom water in March to May and the salinity in November to December. Hile (1941) found that average air tempera-

tures in June and September and rainfall were both important factors in governing productivity of Nebish Lake rock bass. Anderson (1951) found that strong year-classes were dependent on high temperatures at spawning and the supply of food during certain periods of life, and that growth was dependent on water temperature and the size of the stock. When more becomes known about fish populations, it will probably appear that the productivity of all of them is governed by a whole array of factors. The very important point that follows immediately from acknowledgement of the existence of such an array is that the various factors must have a joint, as opposed to an additive net effect. The number of fish killed by cannibalism will not be independent of the number killed by man or birds, since the several kinds of mortality factors compete with each other for fish to kill. The effect of temperature on growth will depend on stock size and the pathogen level, amongst other factors. Admission that such joint operation exists affects the way in which we construct our mathematical model of productivity.

The preceding review of factors governing productivity reinforces the argument that a model of productivity must be developed in terms of the stock remaining in the water, not the number and age distribution of stock removed by fishing. It is the former, not the latter that is of importance for the future productivity of the population.

The great number of papers documenting year-to-year variations in the growth rate and survival of year-classes (eg. Anderson, 1938; Fry and Watt, 1955; Hile, 1954b; Rollefson, 1938; Tester, 1951) and the great variations in growth and strength of different year-classes constitute an overwhelming argument in favor of treating year-classes separately in any model of productivity.

It also follows from examination of the preceding list of factors that mean weight and numerical strength of a year-class are affected in different ways and to different extents by two sets of factors which may only partially overlap. Hence mean weight and numerical strength must be treated separately in the productivity model.

Finally, three characteristics which any realistic model must possess are determined by economic characteristics of the fishing industry and the biological character of the productivity phenomenon. For economic reasons, it is not feasible to attempt certain possible techniques for maximizing productivity of fish populations. For example, supplementing the natural fecundity of a population with hatchery planting of fry is out of the question for an oceanic fishery and many other fisheries; removing part of the spawn to minimize deleterious competition would be similarly infeasible. Also for economic reasons, certain sizes of fish constitute a desired target of fishing; the productivity theory is of maximum use if it shows how to maximize the productivity of selected age- or size-classes of fish. Last of all, the great number of factors involved in the productivity phenomenon rules out any graphical method of analysis; the technique of determining inflexion points in the productivity hypersurface accurately and objectively must employ the method of partial differentiation.

The above desiderata dictate the form of the model we must have. Let us proceed as follows.

SYMBOLS

- a the age of a year class of fish at a specified point in time
 p the first age at which fish are liable to exploitation by man
 z the last age at which fish are liable to exploitation by man
 ${}_a N_t$ the number of fish of age a surviving to the end of year t
 ${}_a w_t$ the mean weight of fish of age a surviving at the end of year t
 ${}_a s_t$ the probability that a fish of age $a-1$ at the end of year $t-1$ will survive to the end of year t
 ${}_a g_t$ the mean weight increment (growth) of fish of age a at time t from the end of year $t-1$ to the end of year t
 P_t productivity, defined operationally as the difference between the biomass standing crop immediately prior to exploitation at the end of year t and the biomass standing crop left in the water after fishing year $t-1$, for those age classes which are liable to exploitation.

Each value of ${}_a N_t$ and ${}_a W_t$ is a function of many factors that operated during a previous years. However, in order to minimize the number of symbols used in the present illustration, let us classify all the components of a fish's environment into four categories (after Andrewartha and Birch, 1954), and assume that the total quantitative force of the factors in each category may be expressed by a single symbol, or index, for each period.

- A_t an index for the total quantitative impact of weather during year t
 B_t an index for the total quantitative effect of food during year t
 C_t an index for the total quantitative effect of other animals during year t
 D_t an index for the total quantitative effect of the availability of places in which to live during year t .

It should be made clear at the outset of the development of this model that the total quantitative effect of any of these four classes of factors is probably not expressible by a single index. For example, "other animals" can include the effect of such factors as the size of the spawning population, the number of competitors for food of the same species and age, interspecific competitors, predators, parasites and pathogens. In addition, the force of each of the various species involved would probably have to be represented by separate indices for each age class of each species, since all parameters describing an animal are functions of the age of the animal. The mathematical technique for handling the effect of competition on productivity, using separate indices for each age class, has already been demonstrated by Watt (1955).

From the definition for productivity, we may write:

$$P_t = \sum_{a=p}^z {}_a N_t {}_a w_t - \sum_{a=p}^z {}_a N_{t-1} {}_a w_{t-1} \quad (4)$$

The object of work on population productivity is to determine how to manipulate the factors that are liable to control by man so that P_t will be a maximum. In order to do this, we must first expand equation (4) to include the various independent variables and determine the general form which the productivity equation must take. Empirically, the exact form of the final version of equation (4) and the values for the parameters must be obtained through

regression analysis of the data for about 20 or more years, or some combination of deduction and regression analysis. A good and detailed exposition of regression analysis suitable for the biologist may be found in Ezekiel (1942) and an example of the combined deductive and least-squares approach to derivation of a productivity equation may be found in Watt (1955), together with a discussion of the logic of fitting and testing complex hypersurfaces, and testing the goodness of fit. Optimum yield mathematics is discussed by Davies (1954).

After the final version of equation (4) has been obtained, values for the independent variables liable to human manipulation and which maximize productivity may be obtained by taking partial derivatives across the productivity equation with respect to these variables, and setting the resultant equations equal to zero, then solving simultaneously.

We may proceed to obtain the general form of (4) by considering, in turn, numerical strength and mean weight for an age class.

${}_0N_{t-a}$ fish of the year class which were age a in year t were hatched in year $t-a$. The number hatched, and the probability that a fish which was hatched would survive to the end of the year $t-a$ were both joint curvilinear functions of the conditions relevant for growth and survival which were operating throughout year $t-a$. To illustrate, the probability that a fish hatched in year $t-a$ would survive to the end of the year may be written as in (5):

$${}_1S_{t-a} = {}_1S_{t-a}(A_{t-a}, B_{t-a}, C_{t-a}, D_{t-a}) \quad (5)$$

The use of commas within the brackets in (5) is done deliberately, to indicate that the net effect of the interaction of the various classes of independent variables is joint, not additive. The final version of the productivity equation is compounded of a whole series of such terms as the right-hand side of (5). In order to minimize the symbolism in the development of the general form for the productivity equation, no more equations of the form of (5) will be given, although it will be understood that equations of this form are in fact represented by the symbols s , N , w and g in the final equation.

In general, the probability that fish of age i will survive from one year to the next is given by

$${}_iS_{t-a+(i-1)}$$

and the probability that a fish born in year $t-a$ will survive to the end of year t is the product of all such terms. Hence the number of fish hatched in year $t-a$ surviving to the end of year t may be given by:

$${}_a N_t = {}_0 N_{t-a} \prod_{i=1}^a {}_i S_{t-a+(i-1)} \quad (6)$$

The expression for the mean weight of the survivors of the year class hatched in year $t-a$ may be derived similarly, to give (7):

$${}_a W_t = {}_1 W_{t-a} + \sum_{i=2}^a {}_i g_{t-a+(i-1)} \quad (7)$$

Finally, from (4), (6) and (7), we get the general form for the productivity equation as (8):

$$P_t = \sum_{a=p}^z \left\{ \left[0. N_{t-a} \prod_{i=1}^a t^{S_{t-a+(i-1)}} \right] \left[1W_{t-a} + \sum_{i=2}^a iG_{t-a+(i-1)} \right] \right\} \\ - \sum_{a=p}^z \left\{ \left[0. N_{t-a-1} \prod_{i=1}^a t^{S_{t-a+(i-2)}} \right] \left[1W_{t-a-1} + \sum_{i=2}^a iG_{t-a+(i-2)} \right] \right\} \quad (8)$$

The technique for using (8) to show how to maximize the productivity of a resource is as follows. While man has no control over certain factors in a fish environment, he can control others, such as the size of the spawning stock. Suppose that analysis of 20 or more years of data has yielded an equation similar in form to (8), and we know, for example, the values of the factors represented by A_t and B_t for the present year. We can substitute these values into (8), and using the technique of partial differentiation, arrive at those values of, say, C_t and D_t which will maximize future productivity.

A numerical example of the derivation and solution of a productivity equation of this type is given in an earlier paper (Watt, 1955) for a laboratory population, and examples of this method applied to natural populations of fish are forthcoming.

It will be clear from the foregoing presentation that I believe the regulation of mesh sizes, and other regulations concerning type and amount of gear should be determined through consideration of the number and age distribution of the fish left in the water by different gears.

The essential difference between the type III model and the type IV model is as follows. The type III model as presently set up shows how to maximize the yield of a year-class that has entered the area where fishing occurs. The type IV model is designed to show how to fish in such a way that conditions in the water make for maximum population productivity in the future. In other words, while type III model in its current form assumes a steady state fishery, type IV model is designed to show how to produce a fishery as productive, and as close to a steady state, as fluctuating hydrographic and non-manipulable biotic factors will allow.

CONCLUSIONS CONCERNING DIFFERENT TYPES OF MODELS

The preceding section of the paper shows that we must be realistic in planning a research program. If we really don't need much information, or a high degree of predictive reliability, it is wasteful to use a research plan based on the more complex types of models, since these require an expensive, comprehensive program of data collection. Conversely, if we do require a high degree of predictive reliability, and a lot of information about the population dynamics of the exploited species, we can not expect to achieve these ends unless we are prepared to maintain a costly and extensive field program. Furthermore, it should be emphasized that the complex, expensive program will probably have to be kept in operation for at least 20 years before it justifies its existence, in

order that enough data can be collected to sort out the effects of all the independent variables, and study the pattern of the way in which they interact. Finally, the whole program will have to collect data at a sufficiently high rate that the results of the work will not defy analysis due to small-sample error. This latter problem will be discussed at the end of the next section.

The researcher must decide exactly what he wants to know, and how much it is worth to have high predictive reliability. If it is worth a great deal, and funds to support an expensive program are available, he should feel committed to one of the more complex models which require a long and costly procedure; otherwise anything more than a design based on model types I or II is not justified by the aims of the program.

One very noteworthy point is that as the progressively more complex types of model are chosen, the data needed for solution are adequate to also allow solution of the simpler types of models. For example, if model type IV is chosen as the basis for the field program, the data collected will be adequate to solve all four types of models. Hence choice of the more complex types of models confers three distinct advantages.

1. Higher predictive reliability.
2. More insight into the dynamics of the population.
3. More approaches can be applied to solution, and as a result the findings from the different models can be checked against each other.

OBTAINING DATA FOR THE SOLUTION OF MATHEMATICAL MODELS

TYPE I MODEL

The major problem with this type of approach is due to assumptions inherent in the use of the instantaneous fishing mortality rate and the catch per unit effort.

If these two indices are to have the meaning assumed by theory, they should only be functions of stock and should be independent, for example, of hydrographic factors, and qualitative changes in gear.

The fact of the matter is that instantaneous fishing mortality rate and catch per unit effort are both affected by seasonal temperature cycles and many other factors (Jensen, 1939), including plankton abundance (Hardy, 1936). For example, as the water becomes colder in fall and winter, fish may tend to aggregate. When this happens, they may become more likely to capture than in summer by any one who knows by experience or use of an echo-sounder where they are aggregating.

Also, catch per unit effort may be related in a complex joint manner to the interval between clearing of the nets and the population density (Kennedy, 1951). Cotton, linen, multifilament and monofilament nylon all have different catchabilities. Fishing power may be related to size of trawler, and angling efficiency decreases as number of men per boat increases.

There are two possible approaches to the analysis of catch-effort data.

1. The first is to develop a complex system of weighting. The weakness in this technique is that if the data have to be stratified by a large number of factors which govern catchability, the amount of data left in any category may be quite small. Sampling variability may then mask the pattern of interaction of the several independent variables.

2. The second approach is to assume that the proportion of different types of effort remains the same from year to year. Conversion factors are only used when there are major changes in the industry, such as a ubiquitous conversion to nylon webbing.

An example from the South Bay data will show first, how the assumptions underlying approach no. 2 may be incorrect, and second, how approach no. 1 is applied in an actual case.

The raw data are in rows 1 to 4 of Table I. We could get an estimate of the pounds per lift during June and July by dividing the total poundage taken by the total number of lifts in June and July. The simple means which result in row 7 suggest that on the basis of this one net there were 85 per cent as many fish present in 1954 as in 1953. However, these indices are totally misleading.

TABLE I. Cisco landings in pound net 5 in South Bay during 1953 and 1954.

	1953	1954
1. Pounds taken during June	6003	4669
2. Pounds taken during July	351	366
3. Lifts during June	8	6
4. Lifts during July	6	7
5. Pounds taken in June and July	6345	5035
6. Lifts during June and July	14	13
7. Pounds per lift during June and July	454	387
8. Pounds per lift in June	750	778
9. Pounds per lift in July	59	52
10. Weighting factor for lifts in July	12.7	15.0
11. Weighted pounds per lift in June and July	744 ^a	779 ^b

$$^a(750)8 + 12.7(58)6 = 744$$

14

$$^b(778)6 + 15.0(52)7 = 779$$

13

Let us pursue the analysis a little further. Rows 8 and 9 give the pounds per lift in June and July, respectively. We see that in both years the availability of fish was much less in July than in June, presumably due to some behavioral factor. In this case the decreased availability is due to movement into deeper water in response to increasing temperature. Obviously a shift from year to year of the bulk of the effort from June to July would result in a decreased annual catch per unit effort. We can correct for this by weighting the July catches in each year by the effectiveness of July fishing relative to the effectiveness of June fishing in the same year. The weights are given in row 10, and applied in row 11. The resulting annual indices of catch per unit effort give a very different picture than the unweighted means in row 7. The row 11 figures show that the abundance as measured by this net actually increased by 5 per cent from 1953 to 1954.

It should be noted that all mention of sampling error is omitted from the above example, for the sake of brevity and in order not to introduce a complicating distraction from the main point.

This example illustrates the technique of weighting catch-effort data. Unfortunately, there are generally several factors for which we should weight, and it is difficult to know where to draw the line. In general, we should probably weight for those factors which have the greatest influence on catch per unit effort, and a shifting frequency distribution of different effects from year to year.

TYPE II MODEL

Type II models, in addition to requiring effort data, use the age structure of the landed catch. This brings up the matter of scale reading.

Gulland (1954) presents a cogent discussion of the bias introduced by ignoring in the calculations otoliths or scales which are difficult, but not impossible to read. He shows that for any length class, the scales which are difficult to read have a higher average age than the average fish in the same class. At larger sizes, the age discrepancy is about four years. Such a discrepancy would have a serious effect on any analysis using age determinations.

Mr. W. J. Christie and the author read the same series of scales independently, and found that our initial impressions of the ages agreed 91 per cent of the time for fish we ultimately decided were four years old, but only 57 to 72 per cent of the time for older fish.

Hence it is a serious error to discard readings for any scales or otoliths, unless they are absolutely impossible to read due to regeneration or mutilation.

The integration of biological and commercial fishery statistics will generally be necessary for getting the age structure from commercial fishery statistics. I maintain that the two items of data we should have on each fish in the biological sample are the weight and the age, not the length and the age. The sample is to be used to interpret the landed catch, and catch statistics are expressed in pounds or tons, not miles of fish laid end to end. The length-to-weight conversion introduces its own sampling error, so it seems logical to avoid it altogether.

The sample data tell us that where W_s is the total weight of fish in the sample, w_i is the mean weight of fish of age i , and N_i the number of fish of age i examined,

$$W_s = \sum_i N_i w_i.$$

Hence the number of fish of age i in the landed catch is:

$$\frac{W_c}{W_s} N_i$$

where W_c is the weight of the landed catch.

Whether an apparent "annulus" in a scale does indeed correspond to a year of growth may be determined by injection of a non-harmful compound that is deposited in all hard structures (Hiyama and Ichikawa, 1952, 1953).

TYPE III MODEL

Type III models, like type IV models, require the age structure of the stock in the water. There are three types of techniques for getting at this, all quite sophisticated in conception, and all very difficult to apply properly.

The first approach is through tag and recapture estimation. There is a plethora of excellent theoretical papers on this subject. Recent examples are those of Bailey (1951, 1952), Chapman (1948, 1952, 1954), DeLury (1947, 1951), Leslie (1952), Leslie and Chitty (1951), Leslie, Chitty and Chitty (1953), Moran (1952) and Schaefer (1951). However, it is worthy of mention that there is still a great gap between theoretical work and the practical problems of application of the theory in the field. Instances such as that reported by Wohlschlag (1954), in which a sophisticated theoretical model was applied in practice on a natural field population, are rare.

DeLury (1954) has already pointed out that planning of experiments for population estimation should take population behaviour into consideration. A variety of other factors should also be considered when planning a mark-recapture program, and these will be taken up now.

If the aim is to determine the age structure of the stock, we must collect scales from all fish released and captured, and stratify the analysis by age. However, the tendency of fish to migrate increases with age (Eschmeyer, Daly and Erkkila, 1953; Mraz, 1952; Sette, 1950), and this complicates the analysis after stratification. If a net is set at a certain place, it will probably only catch very young fish if they are in the immediate vicinity, whereas an older fish may be caught within 24 hours of the time of setting the net if it was six or more miles away at the beginning of the period. This means that population estimates based on recaptures from the net set in the same place all season have a different significance for fish of different ages. For example, the tag-recapture estimate of the population of two year olds may refer to a population in seven per cent of the area occupied by the population of seven-year-olds estimated from tag recaptures by the same net.

The field program may be designed to correct for this age-specific migratability by releasing numbered tags on at least a few hundred of the marked fish released and keeping accurate records of the time and place of release and recapture. An alternative technique is to use some clipping code. For example, spine 1 may be clipped for net 1, spine 2 for net 2, and spines 1 and 2 for net 3.

From these data we can get a minimum estimate for the distance a fish of given age travelled in a known time. Presumably, the minimum distances so obtained will be proportional to the total distance travelled, if we pool enough data. Taking the highest distance travelled as having a weight of 1.00, we can derive a system of weights which will give the relative probability of capture of fish of different ages. A sample set of data illustrating the derivation of the weights is given in Table II.

In South Bay, Manitoulin Island, smallmouth bass are caught each year in trap nets and by anglers. The anglers constitute a large, widely spread group

of small units of effort, which may be considered to sample the whole bass population quite thoroughly. Hence the population estimates based on recapture by anglers of tagged fish constitute a good check on the use of the notion of relative probability of capture, based on the mean minimum distance travelled per day. The validity of this notion is illustrated by the array of figures in Table III.

TABLE II. The relative probability of capture of smallmouth bass in South Bay during 1949 as obtained from trap net data.

Age	Number of individuals used in calculations	Mean minimum distance travelled in miles per day	Relative probability of capture
2	8	.008	.07
3	55	.036	.31
4	31	.036	.31
5	53	.090	.78
6	39	.108	.94
7	38	.115	1.00

TABLE III. Estimates of size of population of bass in South Bay in 1954 for individuals of legal length and over.

	Age				Totals
	4	5	6	7	
1. Schnabel estimates from net recaptures	925	1079	530	44	
2. Relative probability of capture	0.31	0.78	0.94	1.00	
3. Relative age composition of net-vulnerable population	2984	1383	564	44	4975
4. Petersen estimates from anglers' recaptures	4800	2600	620	130	8150
5. Absolute estimates from net recaptures	4890	2270	920	70	8150

The row 1 estimates show a different age composition than the row 4 estimates based on anglers' recaptures. If we divide each item in row 1 by the correction factor in row 2, we get the age composition shown in row 3.

It should be noted here why the chance of a fish of given age being caught in a net is being taken as proportional to the mean minimum distance travelled per day. Smallmouth bass are essentially shallow-water fish, and the angling and trap netting for them is generally done in shallow water. I have assumed that bass travel largely by following shorelines. In the case of a deep water fish, the corresponding relationship would probably be, "the probability of capture in an area is proportional to the square of the radius" (from the formula for the area of a circle).

The age composition in row 3 adds up to less than the total population obtained by totalling row 4, presumably due to incomplete sweeping of the bay by the limited number of trap nets. Apparently only 61 per cent of the population vulnerable to angling was vulnerable to nets, and hence a multiplier of

1.64 had to be used to get row 5. Bearing in mind the small sample sizes of the tags released and recaptured, the estimates in rows 4 and 5 agree surprisingly well, and seem to confirm the notion that population estimates based on net recaptures should be corrected for age-specific migratability.

Two recommendations are suggested by this illustration. First, tag-recapture programs that are to be used to get absolute estimates of population size and age structure should make use of numbered tags or some clipping code, and careful records should be kept of the exact time and place of release and recapture. Second, if it is planned to estimate population size from tag recaptures in nets, the nets should be close enough so that all the population in the area under consideration is liable to capture. How close the nets should be has to be determined by gradually setting them closer and closer until a further increase in density of nets produces no increase in the estimated population of any age group.

Another technical problem arises in the marking of very small, delicate fish. Tagging or fin clipping a smelt, alewife, or chub for example would probably result in death soon after the fish was released. However, if man is ever to exploit most efficiently the resources of the world's lakes and oceans, he must get a maximum sustained yield of the small fish that utilize the incident solar radiation close to the base of the food pyramid, and have a biotic potential that staggers the imagination. Therefore, some technique is needed for getting population estimates of these animals by means of mark and recapture, as a check on any estimates made by catch-effort analysis.

What is needed is a cheap, rapid technique for marking, handling and releasing small fish in bulk, while keeping accurate records of the operation. As yet, much too little attention has been given to the possibility of dyeing, staining or coloring these animals in great numbers. Papers by Al-Hamid (1954), Dunn and Coker (1951) and Kusakabe (1953) suggest classes of chemical compounds which are useful for subcutaneous staining. Hickling (1945) and later workers have tattooed fish, and Davis (1955) has successfully injected fish subcutaneously with colored liquid latex.

Three other technical problems should be circumvented through design of the field program. The plan should allow us to sort out the effects of tag loss by the fish while in the water, tag-induced mortality, and tag reportability. Tag reportability refers to the chance that a commercial fisherman will report the finding of a tag to the local biological research station.

The effects of these three factors may be quantitatively assessed through simple modifications of the field program, and the application of simple formulas.

Suppose we release two equal groups of fish marked as follows.

GROUP 1. Tag and one kind of clip.

GROUP 2. No tag and second kind of clip.

Let R_c^1 be the number of group 1 recoveries with tag and clip

R_c^1 be the number of group 1 recoveries with clip only

R^2 be the number of group 2 recoveries.

It is a reasonably safe assumption that fin-clipping does not add to the instantaneous mortality rate, in mature spiny-rayed fish, at least (Ricker, 1949). Hence the chance of the tag being removed from the fish while in the water is given by:

$$\frac{R_c^1}{R_c^1 + R_{tc}^1}$$

and the chance of tag-induced mortality occurring is given by:

$$\frac{R^2 - (R_c^1 + R_{tc}^1)}{R^2}$$

The tag reportability is obtained as follows. Let T_o/S_o represent the number of fish bearing tags as a fraction of the total number of fish in a sample of the landed catch seen by a trained observer stationed at a port. Let T_f/S_f represent the number of tags reported by commercial fishermen as a fraction of the number of fish in the landed catch. S_f , the number of fish in the landed catch, may be obtained by the integration of biological and commercial statistics, as outlined earlier in this paper.

The chance of a fisherman reporting a tag on a fish landed in the commercial catch is given by:

$$\frac{T_f/S_f}{T_o/S_o}$$

An alternative method for determining the percentage tag loss is to use two tags, placed sufficiently far from each other on the body of the fish so that the chance of one tag being lost will not be correlated with the chance of the second tag being lost. Then we may determine the percentage tag loss from the numbers of recaptures in three categories (one tag lost, the other tag lost or neither tag lost) by drawing up a simple probability array, and computing from the conditional, rather than the marginal probabilities. That is, we can determine the loss of tag x from the cases in which tag y was not lost, and the loss of tag y from the cases in which x was not lost.

As DeLury (1954) has stressed, the two commonest types of tagging plan, named after Petersen (1896) and Schnabel (1938), depend on assumptions. The Petersen plan assumes that the proportion of tagged individuals in the population remains constant during the sampling period, and the Schnabel rationale assumes that the size of the population is invariable throughout the sampling period. The assumptions underlying the even more sophisticated tagging schemes, and the routines that must be followed in fulfilling their requirements make them even more difficult to apply in the typical commercial fishery.

In the case of most commercial fisheries, it is difficult or impossible to meet the assumptions of the mathematical theories of tagging and recapturing. If we follow the Petersen scheme, we can not release tags continuously over a period of time concurrently with sampling. This commits us to a policy of either releasing our tags in a terrific burst of effort during a very short part of the fishing season, or else releasing the fish at a more leisurely clip prior to the

opening of the season. The latter procedure maximizes the ever-present influence of natural mortality, due to the time lag between release and recapture. The former, or "burst" procedure is terribly inefficient. A crew must be rounded up, and equipment collected for a great deal of work in a short time. As several of us have doubtless found to our chagrin, when the time comes to capture and mark the x fish that must be tagged in order to produce a statistically satisfactory number of recaptures, the fish miraculously disappear or the weather gets too bad to send anyone out in a boat.

The Schnabel plan assumptions are difficult to meet because both natural and fishing mortality are often concurrent with sampling.

From a practical standpoint, the ideal way to mark and recapture fish for population estimation would be to tag all during the commercial fishing season, as weather conditions and fish availability allowed. Instead of having to muster a quite large crew for a short burst of tagging, a permanent three-man crew could work all year. This would have the advantage of creating a highly skilled and efficient team and would therefore minimize the tagging cost per fish. Also, tagging throughout the commercial season does away with the need for a frantic effort to complete tagging or tagging and sampling prior to the opening of the season.

The following model is proposed as the rationale for a tagging and sampling program in which tagging, sampling, re-releasing and commercial fishing are concurrent. Since it is an unsophisticated deterministic model, it is only proposed as a temporary measure until someone has the time to work out a mathematically rigorous stochastic model.

Let X_i be the number of fish released with tags on day i

N_t be the number of fish in the water on day t

N_0 be the number of fish in the water immediately prior to the beginning of the tagging period

C_i be the number of fish caught and killed on day i

n_t be the number of fish in the sample examined for tags on day t

x_t be the number of tagged fish in the sample on day t

M_i be the number of tagged fish caught and killed on day i .

Then the number of marked fish extant in the water on day t is given by:

$$N_t = \left(\sum_{i=1}^{t-1} X_i - \sum_{i=2}^{t-1} M_i \right) \cdot n_t / x_t$$

The number of fish extant in the water prior to marking was

$$N_0 = \left[\left(\sum_{i=1}^{t-1} X_i - \sum_{i=2}^{t-1} M_i \right) \cdot n_t / x_t \right] + \sum_{i=1}^t C_i$$

The best estimate of N_0 is obtained from the weighted mean of a series of estimates of N_0 , weighting by the sample size.

A number of refinements could be made in this formula, such as introducing a correction for natural mortality. However, whether or not it is worth while to make these corrections will depend on the particular field situation. The

estimate of error depends on the particular version of this basic formula that was actually used in any given instance.

The second type of technique for population estimation is based on the analysis of catch-effort data. Two radically different variations are available. One follows a year-class from year to year (Beverton, 1954) and the other follows a population within a year (DeLury, 1947, 1951). Such methods are liable to the usual sorts of complications which have already been discussed in connection with catch-effort analyses.

The third basic type of approach for obtaining absolute population estimates is combined catch-effort and tagging. The mathematical rationale of the technique and the details of solution have been presented and discussed elsewhere (DeLury, 1951, 1954; Ketchen, 1953) so will not be given here.

There is a final point I should like to stress in connection with estimation of population size and age distribution. As a matter of routine, three or more techniques of estimation should be used, all based on quite different assumptions. When we consider all the possible sources of error in the various techniques, it is apparent that only such cross-checking will allow us to have any real faith in the results.

TYPE IV MODEL

All the techniques for estimating the size and age composition of populations have now been mentioned. In the solution of model type IV, it may be necessary to apply these methods to not only the population for which we desire the productivity equation, but also the populations competing with it, preying on it, and preyed upon by it.

In addition, records on temperature, water currents, chemical composition of the water and other factors may be necessary in order to get the maximum predictive reliability out of the type IV approach. However, records other than the usual meteorological records kept by government weather bureaus may not always be required for all factors, although this point should be checked adequately. In one study (Fry and Watt, 1955), we found that the relation between air temperatures measured at Dominion weather stations many miles away and the surface water temperature near the laboratory was essentially straight linear for most of the year.

However they are obtained, quite comprehensive sets of daily hydrographic readings should be collected as an integral part of every program of collection of field data. The need for hydrographic measurements is made clear by the list of factors known to influence productivity in some cases presented earlier in this paper.

DETERMINING SAMPLE SIZE

There is no need to outline the computational techniques for deciding how many tagged fish should be released. The problem of sample error in tagging

programs has been quite admirably discussed by the authors mentioned at the beginning of the section on the solution of the type III model.

However, another problem that is quite difficult to handle will be treated. Model types II, III and IV require that we know the age structure of either the landed catch, or the fish in the water. From how many fish must we remove and read scales or other bony structures in order that we will know the age structure of the population with prespecified precision and reliability?

Three factors are known to determine the size of the scale sample that must be collected, and others will probably be discovered.

1. Random sampling error.

2. Schooling behavior may affect sample size needed. For example, if fish do not school randomly with regard to age, then two different kinds of sampling error must be considered. Error is introduced by taking a sample of schools, and a sample of fish from within schools. To illustrate, if old fish tend to stay with each other, the estimate of mean age for the population would be badly biased if the field staff happened to sample a series of schools containing a preponderance of old fish.

3. The estimate of the minimum number of scales that should be collected will be badly in error if only a fraction of the scales collected can be read. Scales with regenerated centers, for example, can not be read accurately.

The statistical procedures for accounting for sampling error, schooling behavior, and inability to read certain scales are as follows.

If there is indeed no schooling behaviour complication and all scales are readable, sampling size can be calculated by means of "Student's" t distribution. Let the frequency of fish of age a in a sample be f_a . Then from the formula for the variance of a binomially distributed frequency,

$$\sigma_{f_a}^2 = \frac{f_a(1 - f_a)}{N},$$

where N is the total sample size. If the allowable fiducial limits are l units on either side of the mean value for f_a , the required sample size to get f_a within the limits $f_a - l$ and $f_a + l$ with a probability of 0.99 is

$$N = \frac{6.76\sigma^2}{l^2}$$

The theory underlying this procedure may be found in any statistical textbook. See, for example, pages 456-458, in the fourth edition of Snedecor's "Statistical Methods" (1946).

The effect of schooling behavior on variability of frequency of an age group may be illustrated by an example from a creel census fishery. Thirty samples of 10 fish each were selected randomly from each of 30 different catches of smallmouth bass made in South Bay in 1953. The actual variance of the frequency of 6-year olds in the 30 samples was 0.048, whereas the theoretically expected variance of the frequency of binomially distributed 6-year olds is pq/n , or 0.022. The reason for the discrepancy is set forth in Table IV.

TABLE IV. The distribution of the frequency of 6-year-old smallmouth bass in 30 samples of 10 fish.

Frequency of occurrence of 6-year-olds	Actual number of samples with this frequency of 6-year-olds	Number of samples with this frequency of 6-year-olds predicted from binomial expansion
.0	5	.6
.1	2	2.9
.2	5	6.2
.3	4	7.8
.4	5	6.7
.5	2	3.8
.6	6	1.5
.7	1	.4
.8	—	.1
Totals	30	30.0
Mean	0.327	

The formula for calculating the terms in the third column of Table IV is

$$30 \left[\frac{10!}{x!(10-x)!} 0.327^x 0.673^{10-x} \right]$$

It will be noticed in Table IV that there were too many samples with no 6-year-olds at all, or 6 or 7 6-year-olds, for the empirical distribution to approximate a binomial distribution. This means that 6-year-olds tend to associate with each other to a greater extent than they would if association was random with respect to age. Hence in this case, schooling is a form of "contagious" distribution of the type discussed extensively by Cole (1946). Yamanaka (1953), using an entirely different statistical argument, concluded that Japanese sardines of the same size tended to school together.

In order to allow for this factor tending to increase the variance of the frequency of an age group, f_a , in samples, σ^2 in

$$\frac{6.76 \sigma^2}{l^2}$$

should not be obtained from the formula

$$\sigma_{f_a}^2 = \frac{f_a(1-f_a)}{N},$$

but rather from

$$\sigma_{f_a}^2 = \frac{\sum f_a^2 - f_a \sum f_a}{N-1},$$

where \bar{f}_a is the mean frequency of age group a . This is a convenient computational formula for the variance.

Dr. D. B. DeLury (personal communication) points out that the effect of schooling behavior on inflation of the variance may fluctuate through time. Factors extrinsic to or intrinsic in the population may govern the amount by which the variance exceeds that expected from chance alone. For example, the degree of contagiousness of distribution on the basis of age or size may in turn

be governed by water temperature or spawning behaviour. Hence the problem of determination of necessary minimum sample size is enormously more complex than it appears at first glance, and solution requires carefully planned sampling experiments which take samples at different times, places and depths. It should be assumed in all cases that the sampling variance will be inflated because of interplay between fish behavior and methods of capture, both of which factors combine to violate the condition of randomness of sampling.

Finally, suppose that from consideration of sampling theory, using an empirical variance to include the effect of schooling by ages, we have derived a value N . N is the number of scales that must be read to give the proportion of each age in the population with predetermined precision and reliability. We have already mentioned that some scales are difficult to read, but should be read to avoid bias. There is another class of scales which is absolutely impossible to read, due to regenerated centers or some other disfigurement. Suppose the fraction of the total number of scales in this category is empirically determined to be x . Then the total number of scales which must be collected in order to give the predetermined precision and reliability is $N + xN$.

SUMMARY

1. The fisheries research program should begin with a carefully conceived plan, in order not to waste time, effort and money by collecting insufficient or superfluous data.

2. The most important element in such a plan is the model to be used in analysis of the data, because the model determines the types and amounts of data to be collected.

3. Four types of models of use in predicting fish catches are already in the literature. Two of these are of use in showing how to maximize the productivity of a resource.

4. The first type of model requires only information on effort, catch, and the instantaneous fishing mortality rate. It does not require the age structure of either the catch or the fish in the water.

5. The next most complex type of model requires information on total effort and the age structure of the catch.

6. The third type of model uses data on the instantaneous fishing mortality rate and natural mortality rate and recruitment, and the age structure and growth rates of the fish in the water.

7. The most complicated type of model requires data on population size and age structure before and after fishing, growth rates, and all factors which can govern the survival and growth of year classes.

8. In general, it is much easier to get the data required to solve the simpler models, but they yield much less predictive reliability and insight into the dynamics of the exploited populations.

9. The most complex type of model is not derived deductively, but its form is obtained after consideration of the existing literature on factors governing the dynamics of exploited populations.

10. Catch-effort data must be weighted to eliminate the effect of changes in factors other than effort and fish abundance.

11. Failure to read difficult scales introduces bias into estimates of population age structure.

12. Increasing tendency to migrate with increasing age introduces bias into estimates of population age structure based on net-recaptures of net-released fish.

13. The well-designed tag-recapture program should measure the effects of tag loss, tag-induced mortality, and tag reportability.

14. It is possible to obtain population estimates when tagging, sampling, re-releasing and commercial or angling fishing or both are all concurrent.

15. Determinations of the number of scale samples that must be collected consider the effect of schooling being non-random with respect to age, and the inability to read certain scales due to regeneration of the centers.

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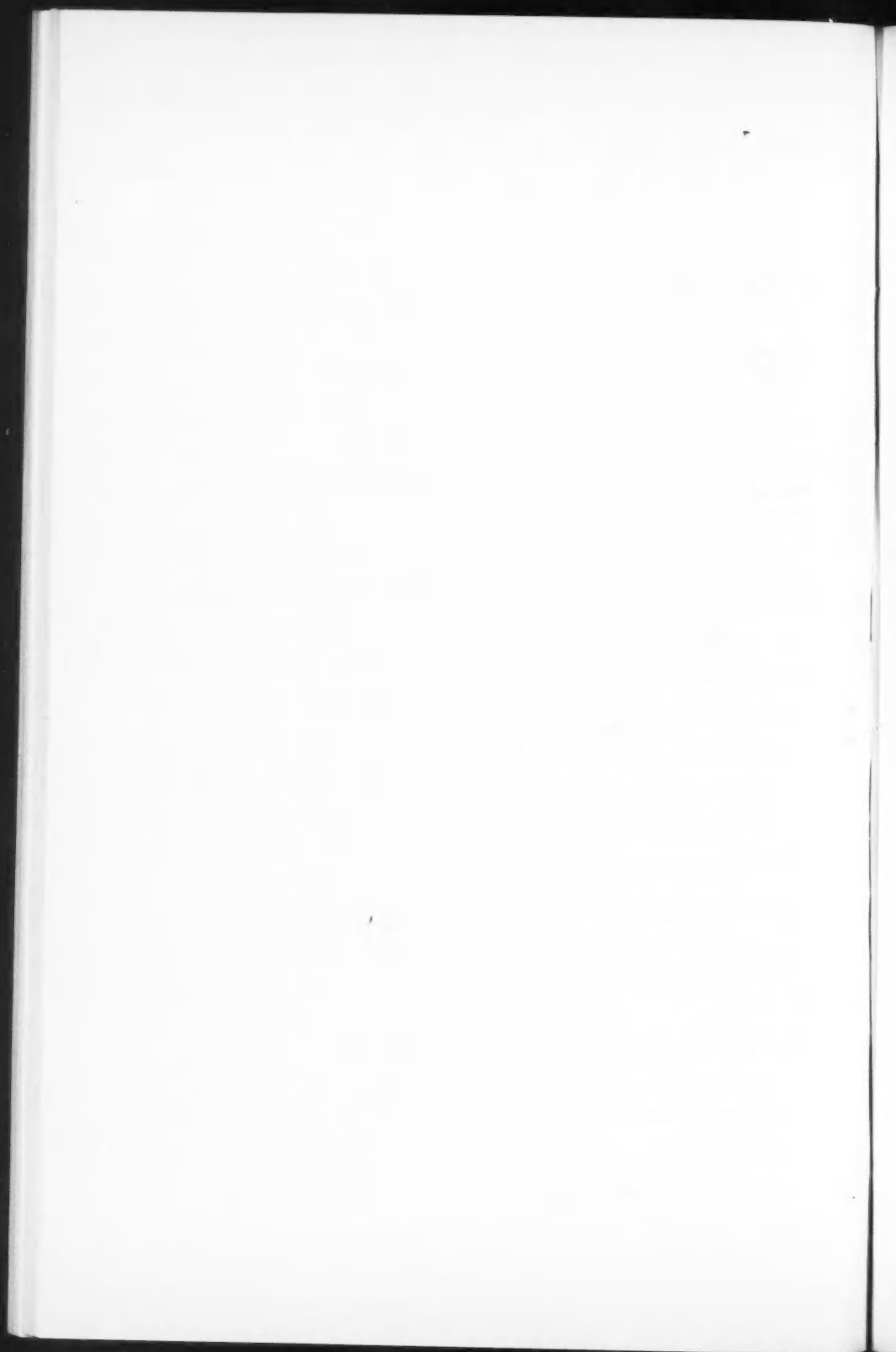
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Factors influencing the survival of the lemon sole (*Parophrys vetulus*) in Hecate Strait, British Columbia^{1,2}

By K. S. KETCHEN³

Fisheries Research Board of Canada

Biological Station, Nanaimo, B.C.

and Department of Zoology, University of Toronto

ABSTRACT

Evidence of fluctuations in the strengths of lemon sole year-classes in Hecate Strait has been obtained from analysis of the age composition of the adult stock during a ten year period. These fluctuations are correlated inversely with sea surface temperatures at the time in the life-cycle when the young are in the pelagic stage. Explanation of this relationship is based on evidence that the young are transported by a northward moving current, from a spawning ground somewhere in southern Hecate Strait to a restricted nursery area lying along the northeastern shores of the Queen Charlotte Islands.

From the results of laboratory experiments on the effect of temperature on the rate of growth of lemon sole embryos, it is concluded that small annual differences in sea temperature produce marked differences in the duration of the pelagic stage. Hence, in years when temperatures are below average, the larvae are carried for a longer period by the northward moving currents. It is maintained that this results in a greater deposition of young on the nursery ground.

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³Address: Biological Station, Nanaimo, B.C.

INTRODUCTION

AFTER many decades of intensive research in various parts of the world, it is now accepted that natural fluctuations in the size of fish stocks are of common occurrence and also that individual year-classes of important food-fishes may vary widely in their numerical strength. The explanation of these fluctuations is one of the most important problems confronting fishery science, for it provides the key to intelligent prediction of the future supply of fish and can, in certain cases, be useful in schemes to control or modify survival. Yet it is noteworthy that, particularly in marine investigations, understanding of the causal factors in population fluctuations has been slow in developing.

A number of serious difficulties confront investigations of this kind. Wholly satisfactory means may not be available to obtain an accurate quantitative expression of the changes in strengths of year-classes. The main obstacle, however, seems to lie in the difficulty of obtaining an accurate description of the environmental events which transpire during that period in the life-history when the strength of a year-class is determined. Even if it is possible to relate these events to the changes in survival, there remains the task of establishing with reasonable certainty that the observed relationships are direct and not merely associated with some still unidentified factor or factors. Thus, it is not surprising, in view of the complexity of the marine environment and the various impediments to precise analysis, that ventures into this field generally have not been successful.

In this paper results are presented of an investigation into the causes of fluctuations in the year-class strength of *Parophrys vetulus*, one of the pleuronectid flatfishes which inhabit the waters of Hecate Strait, British Columbia. From this study it has been concluded that factors which govern dispersal of the pelagic young to their restricted nursery area play a dominant role in survival. The fluctuations in year-class strength have been found to be inversely related to surface water temperatures at the time of the pelagic stage. It is believed that water temperature has a bearing on survival through its influence on growth rate and hence on the duration of the pelagic stage, which in turn determines the extent of dispersal by ocean currents.

The plan of attack consists of three main parts: first, the description of various biological features of the Hecate Strait lemon sole stock, from which conclusions are drawn regarding the life-cycle, spawning area and rearing area; secondly, the description of the process by which fluctuations in brood strength have been assessed; and thirdly, the examination of environmental factors which might have a bearing on survival.

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BACKGROUND

GENERAL LIFE-HISTORY

Parophrys vetulus (Fig. 1) is limited in its distribution to the Northeastern Pacific ocean from the Gulf of Alaska to southern California (Norman, 1934). In Canadian waters it is called the "lemon sole" while in United States waters it is called "English sole".

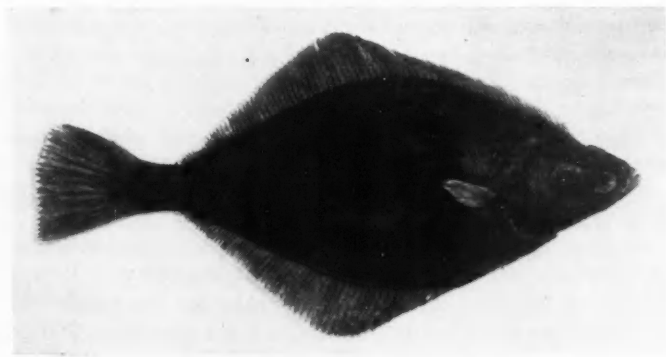


FIG. 1.—The lemon sole (*Parophrys vetulus* Girard).

In comparison with other flatfishes, the lemon sole is an inhabitant of intermediate depths, the adults being encountered usually at depths of 30 to 50 fathoms (60-100 meters). The distribution according to size and age is similar to that of the plaice of the North Sea (c. f. Heincke, 1904; Garstang, 1909) in that the species is found in shallow water close to shore in early life and in progressively deeper water at older stages.

Adult lemon soles are found most frequently in regions where the bottom is of soft sand or mud. They feed almost exclusively on bottom organisms such as polychaetes, pelecypods and ophiuroideans.

Age determinations from otoliths show that the female of the species is faster growing than the male and also tends to reach a slightly greater age (17 years as compared with 15 years in males). The females begin to reach commercial size (30 to 32 cm.) at three years of age, but are not fully acceptable to the market until five or six years of age. The males, because of their much slower growth, do not become completely available before they are seven or eight years of age.

As is the case in many other fishes, the male lemon sole reaches first maturity at an earlier age than does the female. Some are mature at two years of age, while females seldom mature before three or four.

The female produces large quantities of very small eggs. Budd (1940) describes the mature lemon sole egg as being spherical and transparent, with an average diameter of 0.90 mm. (range: 0.89.—0.93 mm.). In British Columbia waters the number of eggs produced by one female at one spawning may range from 0.2 million to 2.1 million, depending on the size of fish. The average appears to be about 1.1 million (Ketchen, 1947).

There is evidence of both inshore and offshore spawning grounds in British Columbia waters. The spawning of inshore populations occurs during the winter months, beginning late in December and ending late in March or early April. The peak time of spawning probably varies from area to area and from year to year, but in the Strait of Georgia it usually occurs early in February.

Inshore populations of lemon sole have definite spawning grounds. In the Strait of Georgia there are two important areas along the east coast of Vancouver Island (Taylor, 1946) and one of minor importance at the entrance to Burrard Inlet near Vancouver. Minor spawning grounds have been found also in four or five inlets bordering on the more exposed parts of the British Columbia coast. All of these grounds lie in relatively sheltered waters (in channels or bights) at depths of 30 to 40 fathoms (60–80 meters) where the bottom is of soft mud.

Little is known of the spawning areas of populations inhabiting the grounds in exposed sections of the British Columbia coast. The fact that large stocks of lemon sole exist off the coast of United States, rules out the possibility that the species is wholly dependent on sheltered regions for spawning. Evidence from tagging studies and from the seasonal pattern of fishing suggests that these stocks move into relatively deep water during the winter months. There is no evidence to suggest that the time of spawning is markedly different from that of inshore stocks.

THE LEMON SOLE STOCK OF HECATE STRAIT

(a) DESCRIPTION OF THE HECATE STRAIT BANK

Off the Pacific coast of Canada the continental shelf is narrow in comparison with that in other parts of the northern hemisphere, and hence the productive

fishing banks are of very limited extent. Three banks exist in the area north of Vancouver Island (Fig. 2) and the largest of these is the one lying in Hecate Strait.

Hecate Strait separates the Queen Charlotte Islands from the mainland of British Columbia and is confluent with Dixon Entrance in the north and Queen Charlotte Sound in the south. A large part of the Strait is occupied by a region of shallow water (average depth 15 fathoms, 30 meters) which results from a broad extension eastward of a bank or shelf from the shores of the Queen

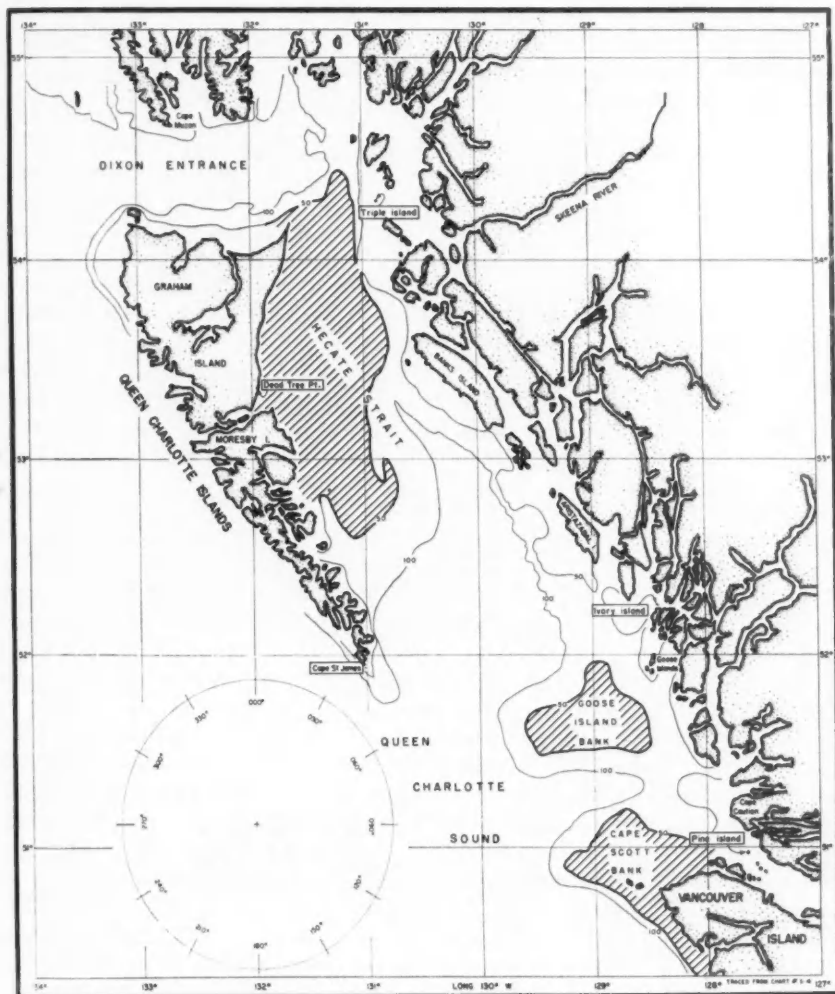


FIG. 2.—Fishing banks along the northern coast of British Columbia.

Charlotte Islands. This bank has an average width of 40 miles and an approximate area of 8000 square miles.

CONTOURS. At the northern end of the Strait the bank projects into Dixon Entrance to form what is known as the Two Peaks ground (Fig. 3). The 20 fathom contour, which passes across the base of the Two Peaks projection, turns abruptly at the Butterworth "corner" and proceeds southward for a distance of approximately 20 miles. The edge of the bank in this region is particularly sharp (see cross-section B in Fig. 3) and is known as the Butterworth ground at its northern end and the Warrior ground at its southern end. South of the Warrior ground the edge of the bank projects towards Banks Island on the mainland side of the Strait (White Rocks ground) and then turns southwestward into the lower central region where are located the Cumshewa and Horseshoe grounds.

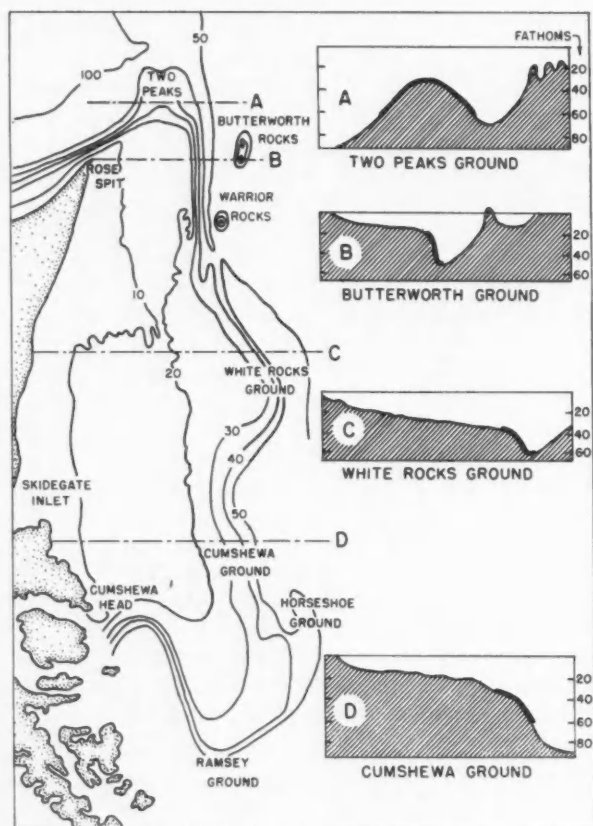


FIG. 3.—Depth contours on the Hecate Strait bank and cross-sections of the more important fishing grounds. Heavy lines in the cross-sections indicate range of depths frequented by adult lemon soles.

The lower half of Hecate Strait has not been thoroughly charted and the contours shown in Figure 3 for the region south of the White Rocks grounds have been constructed from information provided by fishermen and from other unofficial sources. These agree in general with the outline shown by Thompson (1915).

TYPE OF BOTTOM. In general those regions lying at depths less than 30 fathoms are very rough, being composed of gravel, shale, shell and barnacles. Towards the northern part of the bank, however, there are greater areas of smooth sand. On the edge of the bank in most regions the composition changes from gravel and hard sand to soft sand and mud as the depth increases. Otter-trawls are the only type of gear used for the capture of lemon soles and other small flatfish species, and hence their activity is restricted largely to several areas along the edge of the bank where the bottom is sufficiently smooth. It is on the Two Peaks ground and along the sharp edge between the Butterworth Rocks and the Warrior Rocks that the main trawl fishery occurs. A small ground adjacent to the northern end of Banks Island (White Rocks ground) extends for about 10 miles along the edge of the bank, but is of only minor importance. Progressing southward from this region there are approximately 20 miles of the edge which are largely untrawlable. However suitable trawling bottom exists further to the south on the Cumshewa and Horseshoe grounds. The remainder of the southern edge, running from the Horseshoe to the Ramsey ground and thence to Cumshewa Head on Moresby Island is generally too rough for trawling. On the eastern side of the trough which separates the Hecate Strait Bank from the islands along the mainland, the bottom is too rough and rocky for trawling (except in the neighbourhood of the White Rocks ground).

(b) HABITAT OF THE ADULT LEMON SOLE

Almost all of the annual catch of lemon sole comes from a relatively small section of the Hecate Strait bank. This lies between depths of 25 and 50 fathoms along the edge of the bank from the Warrior Rocks to the Two Peaks grounds. Relatively small catches are made in regions south of the Warrior grounds. However, a few adults occur on the White Rocks grounds and in the vicinity of the Cumshewa and Horseshoe grounds.

The very limited extent of the trawling areas for lemon sole in Hecate Strait is determined to a large extent by the tendency for the adults to remain throughout the fishing season (March to August) at depths of 25 to 50 fathoms. Hence, they are confined in their distribution well to the eastern side of the Strait. Localized fisheries in shallow water (10 to 20 fathoms) produce only minor quantities of this species. Its scarcity (in the adult stage) in these regions has been confirmed by exploratory fishing of the *Investigator No. 1*, a research vessel of the Fisheries Research Board of Canada.

This confinement to the deeper water around the northern end of the Hecate Strait bank applies to the spring and summer months of the year. Evidence of migrations away from this area during the fall and winter months will be discussed in a later section.

(c) THE FISHERY

The history of the Hecate Strait trawl fishery for flatfish may be divided into two periods, both of which were associated with economic conditions arising from the two World Wars. The first exploitation by trawlers took place in 1913 and catches of flatfish (all species other than halibut) rose to a peak of about a million pounds per year by 1919. After that year, however, a sudden decline in demand caused landings to fall sharply and to remain negligible (less than 100,000 pounds per year of all species) for 23 years (1920-42). During World War II a re-awakening of the demand for flatfish fillets resulted in an extensive development of the Hecate Strait and other fisheries about 1943 or 1944.

Table I shows the Hecate Strait catches of lemon sole as estimated from statistics of the Canadian government Department of Fisheries, the State of Washington Department of Fisheries and from records collected by the Fisheries Research Board of Canada (Nanaimo Biological Station). The last mentioned have provided additional information on catch-per-unit of effort, beginning in 1945.

TABLE I.—Annual total catch and seasonal average catch per unit of effort of lemon sole from Hecate Strait, British Columbia.

Year	Total catch	Canadian catch per hour of trawling
	<i>thousands of pounds</i>	<i>lb. per hour</i>
1942	(100) ^a	?
1943	(400)	?
1944	(550)	?
1945	(810)	1,200
1946	(1,432)	820
1947	(992)	850
1948	2,193	680
1949	2,358	590
1950	5,780	1,210
1951	2,257	750
1952	2,945	640
1953	2,214	720

^aFigures in brackets are approximations.

Following the initial expansion, the annual catch fluctuated between one and two million pounds for a period of 5 years ending in 1949. In 1950 an exceptionally heavy fishery occurred as a result of the combined influences of a high availability and a greatly increased fishing effort. In the following year however, the catch assumed the magnitude of those in the years leading up to 1950.

The fishery for the lemon sole occurs usually during the late winter and spring months (Fig. 4). Although weather has an effect in restricting fishing during the winter months, there is considerable evidence that the spring increase in catch is related to an increase in catchability as the fish move on to the

fishing grounds. This was particularly evident in the 1950 fishery (Ketchen, 1953: 471). The month of peak production depends greatly on the pattern of fishing effort; during all but one of the past eleven years (1944-1954) it has been either in April or May. Declining production during mid-summer months is the result of declining catchability as the fish become dispersed and also the result of the increased attractiveness of fisheries for other species.

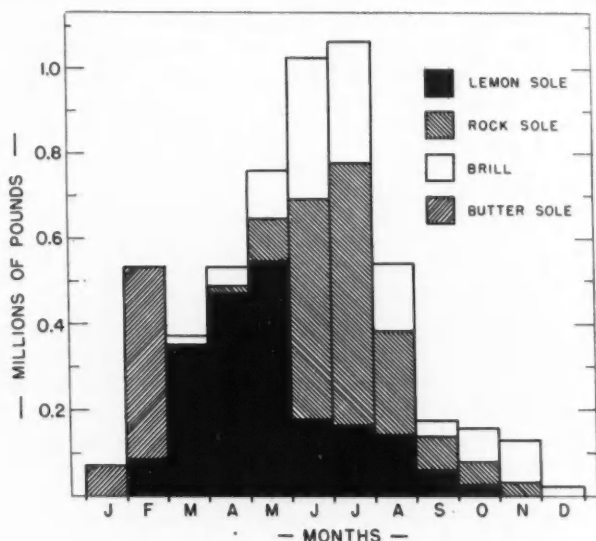


FIG. 4.—Average monthly landings of flatfish by Canadian trawlers operating in Hecate Strait (1948-51, inclusive).

SPAWNING AND NURSERY GROUND RELATIONSHIPS

Before investigating the factors which might play a role in governing the strength of a lemon sole year-class, we must consider the spatial and temporal positions of those stages in the life-history where the success or failure of a year-class is likely to be determined. Can it be demonstrated that the critical stage (presumed to be the pelagic stage) occurs within the bounds of Hecate Strait? Can it be demonstrated that the early bottom stages, if present in the Strait, eventually become recruited to the adult stock from which the estimates of year-class strength are to be derived? Furthermore, can it be demonstrated that these young fish are the progeny of the adult fish in the Strait? Answers to these questions will arise from consideration of (1) the position of the main spawning ground, (2) the position of the main rearing area, (3) the mechanisms connecting these two regions and (4) the geographical pattern of recruitment into the adult stock.

(a) POSITION OF THE MAIN SPAWNING GROUND

The location of the main spawning ground of the lemon sole in Hecate Strait must be inferred from the movements of spent and maturing fish since it has never been established by direct observation of fish in the process of spawning. Mature lemon soles disappear from the Hecate Strait bank during the winter months. When they reappear in the late winter and early spring nearly all are in a freshly spent condition. This phenomenon is common to offshore populations of other flatfish along the Pacific coast of North America and accounts to a considerable extent for the seasonal nature of the fisheries.

Petersen-type disc tags were employed in tagging the lemon soles of Hecate Strait. Attachment was made at a point just posterior to the head and below the dorsal fin—a technique which has been found to interfere least with the activity of the fish (Manzer, 1952).

MIGRATIONS ON THE NORTHERN GROUNDS. In the month of April, 1950, 3000 fish were tagged, of which 1630 were released southwest of the Warrior Rocks and 1370 were released southwest of the Butterworth Rocks. The distance separating these two areas was approximately 15 miles.

The pattern of recaptures by the fishing fleet in the four or five months following tagging near the Warrior Rocks is illustrated in Figure 5. Recoveries with known position have been assigned to four-mile divisions of the bank lying between the Warrior grounds and the Two Peaks grounds. The results showed a pronounced northward movement of the stock. During the summer months most of the recoveries were made on the Two Peaks ground, 25 to 30 miles to the northwest of the point of release.

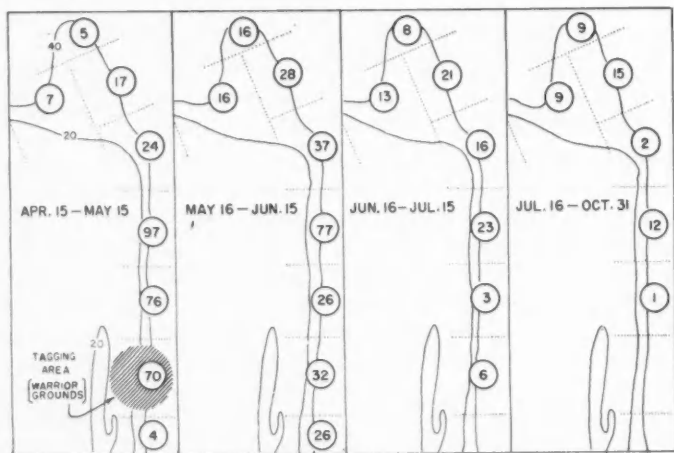


FIG. 5.—Pattern of tag recoveries from 4-mile sections of the Hecate Strait bank following release on the Warrior grounds between April 7 and 20, 1950.

The recoveries from the Butterworth Rocks tagging showed less evidence of a northward movement during the first two months, but the general pattern was the same.

The decrease in number of recaptures as the season progressed and the decline in the commercial catch suggests that the stock moved out of the range of the fishery during the summer months or became dispersed on the Two Peaks grounds to such an extent that its exploitation was no longer practicable. The latter possibility is the most plausible. Since the lemon soles in Hecate Strait generally inhabit depths from 25 to 50 fathoms, they would be less densely concentrated in regions where the slope of the bank is slight than in regions where it is relatively steep. The difference in the slopes of the bank in the Butterworth and Two Peaks regions has been shown in Figure 3. Once the fish leave the confines of the Butterworth and Warrior grounds (6 square miles) and move on to the Two Peaks ground (19 square miles), many of the trawlers turn to the more lucrative fishery for rock soles which develops on the Butterworth edge of the bank (15-20 fathoms) during the summer months.

From information provided by trip reports, it is apparent that the lemon sole moves from deep to shallow water with the advance of spring (Fig. 6). This suggests that the migration does not continue beyond the Two Peaks into the deep water of Dixon Entrance.

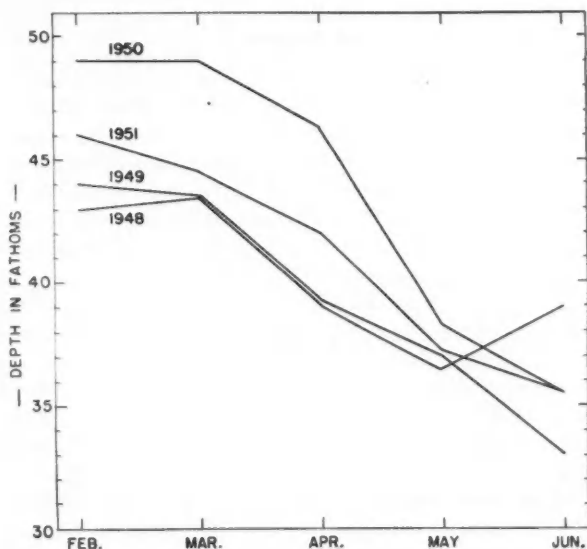


FIG. 6.—Trend in average depth at which lemon soles were caught by Canadian trawlers during the late winter and spring in Hecate Strait.

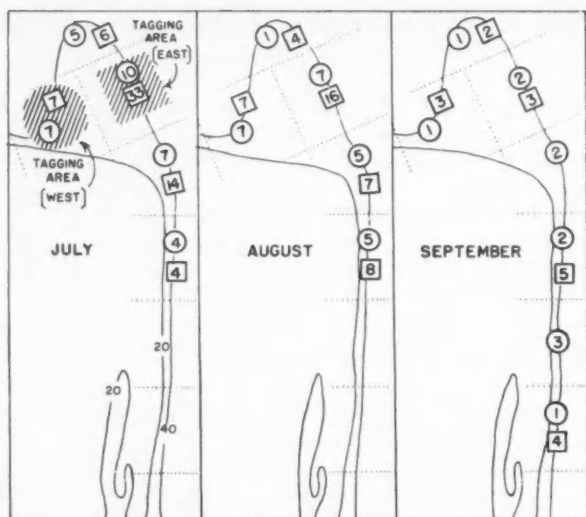


FIG. 7.—Pattern of lemon sole tag recovery from 4-mile sections of the Hecate Strait bank following release on the Two Peaks ground in June 1952. Circled numbers correspond to the western tagging area, while those in squares correspond to the eastern area.

Evidence that lemon soles remain on the Two Peaks ground during the summer months was shown by tagging conducted in that area in June, 1952. The recaptures from a release of 1975 tagged fish showed considerable mixing within the Two Peaks–Butterworth region during July and August (Fig. 7) and some suggestion of a southerly movement in September. During October and November 5 out of a total of 34 recaptures were made on the White Rocks ground, about 75 miles south of the tagging areas.

These observations may be summarized as follows: (1) there is a northward migration in the spring months which begins at least as far south as the Warrior grounds; (2) this movement seems to terminate on the Two Peaks ground during the summer months; and (3) there is evidence of a southerly or return movement in the early fall. Since these fish which participate in the northward migration in the spring are in a freshly spent condition it must be presumed that the spawning area lies somewhere to the south of the Warrior grounds.

MIGRATIONS ON THE WHITE ROCKS GROUND. As already stated, large sections of the edge of the Hecate Strait bank, although probably providing suitable cover conditions for migrating lemon soles, are too rough or uneven for trawling. This situation exists along the edge of the bank for a distance of 20 miles immediately south of the Warrior grounds. The nearest region which is comparable

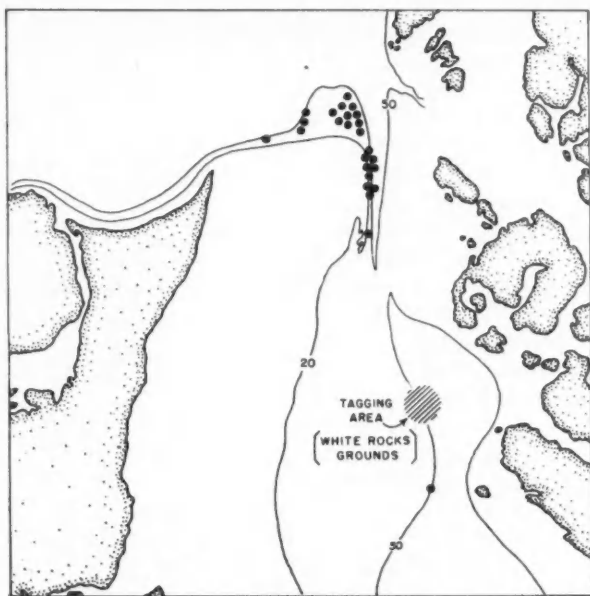


FIG. 8.—Pattern of lemon sole tag recovery during the period April to August, 1951, following release on the White Rocks ground early in March, 1951. Each dot represents one recovery.

in extent to the Warriors is the White Rocks ground. In this area, adult lemon soles are taken in the late fall and winter months, in small quantities incidentally to the fisheries for brill (petrale sole) and dogfish. Although samples of maturing fish have been taken from this area in the fall, no spawning fish have been encountered in the winter catches.

At the beginning of March, 1951, 445 lemon soles were tagged and released on the edge of the White Rocks ground. The recovery pattern which followed in the spring and summer of that year was again indicative of a northward movement (Fig. 8). Between April and August, 25 tagged fish were recaptured on the grounds lying between the Warriors and the Two Peaks, a distance of 40 to 60 miles from the place of tagging. Similar results were obtained from a small tagging in February 1947. This suggests that the spawning ground lies at least as far south as the White Rocks ground.

MIGRATIONS ON THE SOUTHERN GROUNDS. A number of factors have made it impossible to trace the movements of lemon soles into the more southerly regions of Hecate Strait. Foremost among these is the weather. At times of the year when one might expect to find lemon soles on the southeastern edge of the bank (late fall or late winter), or in spawning condition (mid-winter months), the weather

is generally too unsettled to permit most trawlers to venture far from shelter. Also, progressing southward the edge of the bank becomes less and less steep and increasingly rough, thus greatly restricting the possibility of catching the species in adequate numbers. However, a few of the larger United States trawlers operate on the southeastern edge during most months of the year, and it is through them that further clues to the migration have been obtained. A fisherman long-experienced in Hecate Strait trawling has reported that he frequently encounters good catches of large (female) lemon sole, "fat with spawn", on the Horseshoe and Cumsheewa grounds (see Fig. 3) during the fall months. This conforms with the impression that the maturing lemon soles move southward from the Two Peaks grounds in the fall, following the same route along the edge of the bank that the spent individuals follow northward in the spring.

The tagging experiments on the more northerly regions of the bank have not been wholly satisfactory in elucidating this point. Few fish tagged in the spring or summer are recovered in the fall of the year in which they are released. This is mainly attributable to the rapid decline in fishing effort because of the weather. For example, recoveries from the tagging in the spring of 1950 (on the Warrior and Butterworth grounds) ceased in October of that year. Not until the spring and fall of 1951 was there any indication in the recoveries that there had been a migration to the southern region of the Strait during the winter of 1950-51. In the spring of 1951 (a year after release) four tagged fish were recaptured on the Cumsheewa ground and in September and October of that year two were recaptured on the Horseshoe ground. In this same period one fish was recaptured on the Goose Island grounds, 100 miles south of the Horseshoe ground (see Fig. 2) and two tags were returned on the Cape Scott bank, 150 miles south of the Horseshoe and 270 miles south of the point of release. In October 1951 and February 1952 two returns were obtained from the Umatilla grounds, near Cape Flattery, Washington, (550 miles south of the tagging area). These two recoveries are the only ones that have been made outside northern British Columbia waters. To what extent they indicate a mixing with the stocks off the coast of the United States is unknown. It should be emphasized however, that the 11 recoveries discussed above (all from the 1950 experiment and all recovered south of the White Rocks ground in 1951 and 1952) constituted only 6.8% of the total recoveries in those two years. The remainder were taken in the spring and summer months on the grounds in northern Hecate Strait.

THE SPAWNING AREA. The recaptures from the southern Hecate Strait region, sparse though they are in relation to the total recaptures, favour the conclusion that the winter spawning ground or grounds lie in the lower region of Hecate Strait or Queen Charlotte Sound. If the spawning ground were to lie in the region between the Cape Scott and Goose Island banks, evidence of such should have come to light before now, since there is a considerable amount of trawling done in that region in the winter months. The small quantities of lemon sole taken there are usually in a spent condition. Furthermore, extensive tagging conducted on the Goose Island bank has revealed negligible migration into Hecate Strait.

There is, however, a large area of Queen Charlotte Sound and lower Hecate Strait which, because of its distance from shelter, remains untouched by trawlers during the winter months. This region extends from the southeasterly edge of the Hecate Strait bank (between the Horseshoe and Ramsey grounds) for a distance of approximately 100 miles to the northwesterly edge of the Goose Island bank (Fig. 2). On the basis of available data it is concluded that spawning of the lemon sole takes place somewhere in this general vicinity, probably in deep water.

The behaviour of the lemon sole may be somewhat similar to that of the Pacific halibut which is known to spawn in deep water off the tip of Cape St. James. A high proportion of recoveries from tagging on this ground were made to the northward in Hecate Strait (Van Cleve and Seymour, 1953).

EVIDENCE OF INLET SPAWNING. Before leaving the subject of spawning grounds it is important to examine the possibility that the main body of the lemon sole stock in Hecate Strait migrates into adjacent mainland inlets and spawns in those regions. Certainly, in view of the observations of the behaviour of populations in the Strait of Georgia, such might reasonably be expected.

Early in April, 1950, a small stock of spawning lemon sole was encountered in exploratory dragging of the *Investigator No. 1* in an inlet which is an extension of Prince Rupert harbour (25 miles northeast of the Hecate Strait bank. A total of 950 of these fish were tagged. No tagged fish were recovered in that year, except by shrimp trawlers in the inlet. In the following spring however, five were recovered on the Butterworth and Two Peaks ground and four in the inshore region close to Prince Rupert. In 1952, nine recaptures were recorded but all these were from inshore (inlet) grounds.

In view of the very small size of this stock it is highly improbable that it makes a significant contribution to the Hecate Strait fishery. However, the possible existence of several hundred stocks of similar size distributed among the various inlets would, of course, deserve consideration. The main argument against the existence of such stocks is that the majority of the mainland inlets are fjord-like and rocky. A few channels in the neighbourhood of Banks Island which have seemed to hold promise as habitable regions for the lemon sole, have been examined and found to be either too rough for trawling or lacking in evidence of spawning fish.

If the spawning area were restricted to one particular inlet somewhere on the mainland coast, it probably would have been discovered by this date, since the fishermen have thoroughly scouted the possibilities for worthwhile inshore fishing during periods of bad weather.

It is assumed, therefore, that those stocks of lemon sole which occur in the mainland inlets are small and mingle only slightly with the main stock in the open waters of Hecate Strait. Possibly a parallel situation on a larger scale is to be found in the relationship of the Strait of Georgia and Puget Sound stocks of lemon sole to those which inhabit the open waters off the lower British Columbia and Washington coasts. The former are apparently composed of self-supporting units having their own spawning grounds (in channels and inlets) and summer

feeding areas. The release of almost 14,000 tagged fish over a period of ten years on these inshore grounds has yielded only 11 recoveries from the banks off the open coast (Ketchen and Forrester, 1955).

To summarize this section, tagging experiments conducted at various points along the eastern edge of the Hecate Strait bank have revealed a northerly movement of lemon soles through the Strait to the Two Peaks ground during the spring months of the year. Since the fish which participate in this migration are in a freshly spent condition, it is presumed that the phenomenon is a post-spawning movement from some region in southern Hecate Strait. Although there is no direct evidence, the spawning area apparently lies in deep water somewhere between the southern end of the Hecate Strait bank and the Goose Island bank in Queen Charlotte Sound.

(b) POSITION OF THE MAIN NURSERY GROUND

The nursery grounds of the lemon sole, like those of many other flatfishes, are in shallow sandy regions of the coast. In the Strait of Georgia, the early demersal stages (fish less than one year of age and conventionally termed the "O-group") seem to be confined during the summer months to sandy beaches at or near the low tide mark. In Hecate Strait they are to be found in the shallow regions, but not concentrated at the shoreline.

The shallow region along the east coast of Graham Island (Queen Charlotte Islands) plays an important role as a rearing ground for the lemon sole in Hecate Strait. Examination of marine charts of the area lying between Cape Scott on the northern end of Vancouver Island and the archipelago of southeastern Alaska shows not only a very limited region of shallow water but also a very limited extent of sandy beaches. Except for a 50 to 60 mile section of the east coast of Graham Island, between Rose Spit and Skidegate Inlet (Fig. 3), the shoreline is relatively steep and rocky. On the basis of observations in the Strait of Georgia, only the east coast of Graham Island and part of the north coast offer the conditions necessary for the survival and development of the O-group lemon sole in the Hecate Strait area.

Exploratory surveys of Hecate Strait were conducted during the summers of 1952, 1953 and 1954. The sampling gear consisted of a small eastern-style otter-trawl (foot-rope length: 40 feet) hung throughout with one-inch cotton netting of 18 thread. The distribution of sampling stations occupied in these three years is illustrated in Figure 9.

Figure 10 shows the frequency of occurrence of O-group lemon soles at various depths in Hecate Strait. It demonstrates clearly that these fish occur most abundantly at depths less than 10 fathoms and that the outer limit of the distribution is around 13 or 14 fathoms at the time of year when the sampling was carried out (June and July). For safety reasons, it was not possible to obtain comparable data for depths less than 2 fathoms, but it was determined by other means that the young are present in the intertidal zone.

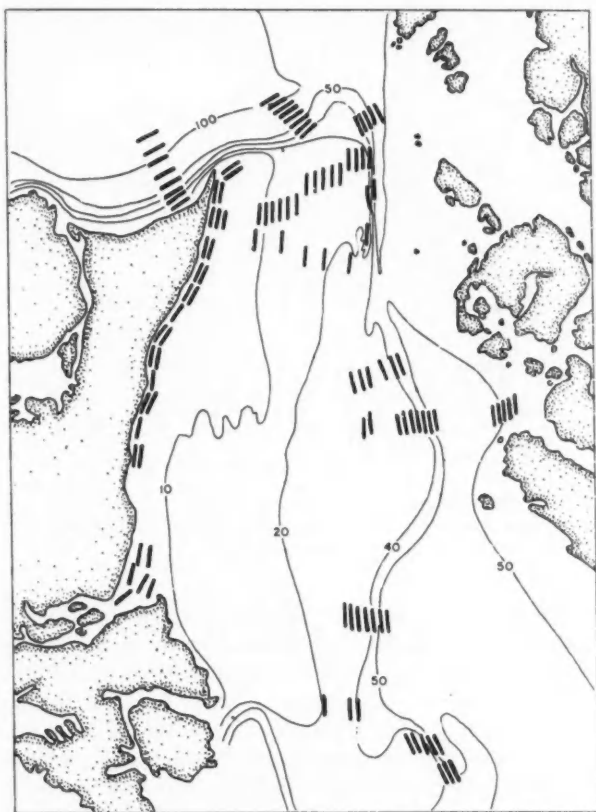


FIG. 9.—Distribution of small-meshed trawl stations in Hecate Strait and Dixon Entrance.

The results of 48 drags at depths greater than 25 fathoms (range 26 to 100 fathoms) are not shown in Figure 10, but these failed to reveal any sign of O-group fish. Thus it may be concluded that the O-group of the lemon sole is limited during the midsummer months mainly to a narrow section of the Hecate Strait bank along the eastern shores of the Queen Charlotte Islands.

(c) RELATION OF O-GROUP FISH TO THE ADULT STOCK

It is important at this point to determine whether or not the stock of O-group fish along the western side of the Strait contributes eventually to the stock of adult fish which is the object of exploitation along the eastern side. On the basis of sampling conducted in the various surveys illustrated in Figure 9, a distribution chart of the various age-groups found around the Hecate Strait

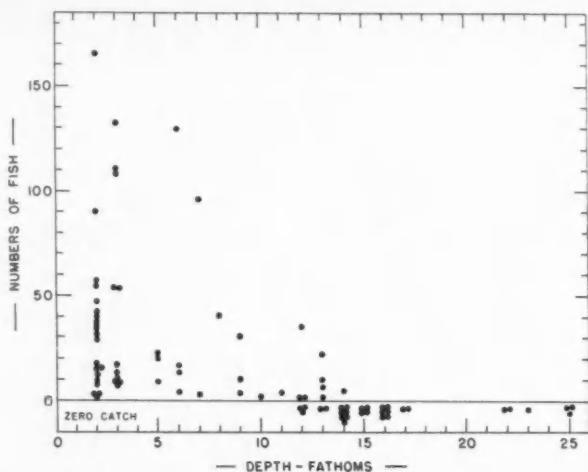


FIG. 10.—Frequency distribution of 0-group lemon soles in 15-minute drags with a small-meshed trawl (June-July period, 1952-54).

bank is shown in Figure 11. The data suggest that I-group fish inhabit a wide area of the "flats", from the shallowest regions along the shores of Graham Island southeastward towards the edge of the bank in the Banks Island and Cumsheewa area. Occasionally they are found as deep as 32 fathoms, but the main summer-time concentrations seem to be on top of the bank at depths less than 20 fathoms.

It is difficult to describe the generalized distribution of older fish, because of their schooling behaviour. Although II-group, III-group, and even older fish are to be found during the summer months over a wide area of the Hecate Strait bank, their main concentration appears to be along the edge of the bank between depths of 20 and 40 fathoms. The II-group and III-group lemon soles are very abundant from the White Rocks grounds southward along the edge of the bank to the Horseshoe. The tendency for fish of sub-commercial size to concentrate on these grounds is well known by trawl fishermen. The mature fish (generally those over age III) are to be found during the summer months in small quantities along the edge of the bank, usually at depths greater than 30 fathoms, but the main concentration is on the Butterworth and Two Peaks sections of the bank (25 to 50 fathoms). As described earlier, it is this body of fish which supports the commercial fishery.

In summary, there is evidence that the adult lemon sole stock present along the north and northeastern edge of the Hecate Strait bank gains its recruits from the shallow region along the east coast of Graham Island. Hence, if fluctuations in year-class strength observed in samples of fish from the former region are determined at an early stage in the life-history prior to the earliest demersal stage (as is here assumed), it is important to consider the mechanisms which lead to the deposition of young along the Graham Island shore. Since the adults

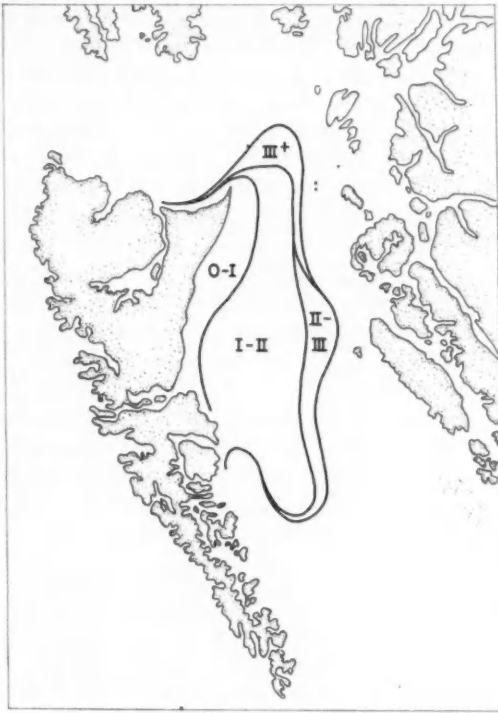


FIG. 11.—Generalized summer distribution of the various age-groups of the Hecate Strait lemon sole stock.

do not frequent shallow water, the eggs and larvae must be transported to that region.

(d) PROCESSES CONNECTING THE SPAWNING AND NURSERY GROUNDS

There is a high probability that the dispersal of flatfish larvae, because of their very small size, is a passive process, dependent on ocean currents. Knowledge of the direction of water currents in Hecate Strait is therefore of importance in determining the origin of the young lemon soles which are present in the shallows along the east coast of Graham Island. Since the effect of currents on translocation of the eggs and larvae from the spawning area is dependent on the depth at which they are suspended, we must first examine certain physical properties of the lemon sole egg.

SPECIFIC GRAVITY OF THE LEMON SOLE EGG. In water free from turbulence it is presumed that eggs of the lemon sole eventually become suspended at depths where the specific gravity of the water is the same as that of the eggs. A laboratory experiment was conducted in which freshly fertilized eggs were placed in seawater solutions of various densities. Observations of their buoyancy in re-

lation to the density of the seawater (at 18.6° C.) are recorded in Table II. In samples 1 and 2, the eggs sank to the bottom of the containers (500 ml. graduates) within a few minutes, while those in samples 3 and 4 remained uniformly distributed for nearly an hour before finally settling out. In sample 5, the eggs rose slowly to the surface of the column, within an hour. Those in samples 6 and 7 rose rapidly to the surface, within several minutes. It would appear then that the specific gravity of the fertilized lemon sole egg is in the neighbourhood of 1.0208 and that the specific gravity of seawater must be greater than this before the eggs can be expected to float at the surface, under conditions of no turbulence.

TABLE II.—Relation of the density of sea-water to the buoyancy of the lemon sole egg.

Sample number	Salinity (‰)	Density (σ_t)	Reaction of eggs
1	27.51	19.5	sank
2	28.43	20.2	sank
3	29.02	20.6	sank
4	29.09	20.7	sank
5	29.25	20.8	floated
6	30.77	22.0	floated
7	31.49	22.5	floated

Table III shows the mean density of the surface seawater at four lighthouse stations bordering on Hecate Strait for that time of the year when one would expect the eggs of the lemon sole to be adrift. Clearly, the density in the surface regions is much greater than the minimum observed in the laboratory to be necessary for floatation. This leads to the conclusion that in Hecate Strait, eggs of the lemon sole would rise from the spawning grounds into the surface waters. Of course, the extent of the concentration at the surface would be governed to a large extent by the amount of turbulence. Buchanan-Wollaston (quoted by Graham, 1930) says that the eggs of the plaice in the North Sea congregate at the surface during calm weather but become distributed at all depths when the sea is rough.

TABLE III.—Density of the surface sea-water at lighthouse stations in Hecate Strait.

Station	Mean density (Jan.-Apr., incl.) (σ_t)	Range of the monthly means
Cape St. James	25.5	24.5-25.7
Pine Island	24.7	24.0-25.1
Ivory Island	23.4	21.8-24.9
Triple Island	25.0	24.4-25.6

Evidence from the laboratory study of the low density of the lemon sole egg in relation to that of the seawater in Hecate Strait, cannot be given precise interpretation. Certain complexities may arise from the ability of the egg to make adjustments to the surrounding medium. Walford (1938) was able to confirm

the earlier results of Ehrenbaum and Strodtmann on other species, that the eggs of the haddock adopt within certain limits the specific gravity of the water in which they are fertilized and that they tend to distribute themselves and remain suspended in this stratum. He showed that with increases of less than 2% of the original density of the water, the majority of the eggs can alter their specific gravity enough to remain suspended. With greater increases the majority seem to be unable to make sufficient adjustment and rise to the surface and remain there.

That the lemon sole egg may make a similar adaptation is not doubted, but it seems unlikely that it is capable of making the large-scale adjustments (ca. 20%) which would be necessary in Hecate Strait, before it could remain in the stratum in which it is spawned. It is presumed therefore, that in Hecate Strait the eggs of the lemon sole rise towards the surface, but the extent of the concentration in that region is dependent on the amount of turbulence resulting from wave and tidal action.

RELATION OF CURRENTS TO THE NURSERY AREA. If larvae of the lemon sole float near the surface in Hecate Strait, then clues to the origin of the early bottom stages present along the east coast of Graham Island should be sought in patterns of surface drift in that region. Although no detailed oceanographic surveys of Hecate Strait have been analysed and reported to date, some indication of the probable drift of water in that region is available in the works of the International Pacific Halibut Commission.

In connection with investigations of the distribution of the larvae of the Pacific halibut, current patterns of the northeastern Pacific were mapped during the early 1930's by means of drift-bottle experiments (Thompson and Van Cleve, 1936). Figure 12 has been reproduced in part from figure 19 of Thompson and Van Cleve, and shows the pattern of dispersal of drift-bottles released in the waters lying off the British Columbia coast between March 22 and March 25, 1932.

The returns from Hecate Strait indicated a northerly current. All recoveries came from points of release which were south of Latitude 51° N., and hence well to the south of the entrance to Hecate Strait. Several bottles were found on the northern and eastern shores of Graham Island. The absence of recoveries in Dixon Entrance and Hecate Strait from the release adjacent to Dixon Entrance led Thompson and Van Cleve to conclude that the drift is westward through Dixon Entrance during the spring months.

In another experiment conducted during the late summer months, Thompson and Van Cleve showed a similar northward dispersal of drift-bottles through the Strait. Eight bottles were found along the east coast of Graham Island and all of these had been released south of Latitude 51° N.

The discovery of bottles in various channels of Clarence Strait (the northward extension of Hecate Strait into the Alaskan archipelago) confirmed the results of Haight (1926) which showed that the non-tidal currents of that region set northward.

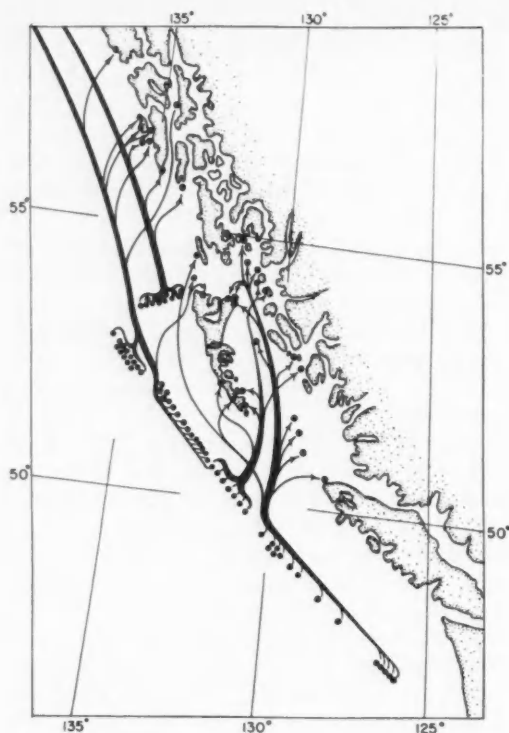


FIG. 12.—Pattern of dispersal of drift-bottles released off the British Columbia coast between March 22 and 25, 1932. (Reproduced in part from Thompson and Van Cleve, 1936).

It is now important to consider these observations in the light of conclusions reached earlier on the distribution of various segments of the lemon sole population in Hecate Strait. The presence in the spring months of a northerly current through Hecate Strait and a westerly current through Dixon Entrance, precludes the possibility that a spawning stock in Dixon Entrance or Clarence Strait produces the young found along the eastern shore of Graham Island. Rather, it supports the conclusions reached from tagging experiments that the young are the progeny of spawning somewhere in the southern part of Hecate Strait or Queen Charlotte Sound. Proof of this relationship cannot be clearly established since both the duration of the pelagic stage and the net rate of water transport at the time of the pelagic stage are imperfectly known. Yet, broad limits can be assigned to these two factors, thus permitting rough estimation of the limits of dispersal. From observations in Georgia Strait it has been noted that metamorphosing larvae make their appearance on the beaches in mid-April and on

occasions at least reach peak abundance by the first week of May. Since spawning on most Georgia Strait grounds reaches a peak around about the middle of February, one may conclude that the period of the pelagic stage lies somewhere within the broad range of 6 to 10 weeks.

Concerning the rate of surface drift, Thompson and Van Cleve limited their discussion to data for the open coast of British Columbia and estimated rates ranging from 10 to 6 miles per day. Data for Hecate Strait alone, dealing with bottles recovered on Rose Spit (their Appendix B, table 24) yielded three estimates averaging 4.0 miles per day (range 3.1 to 5.3 miles per day).

Assuming that the pelagic stage of the lemon sole lasts from 6 to 10 weeks (42 to 70 days) and that the entire period is spent at depths where the current velocity is the same as that registered by the drift-bottles, the distance which a larva might be expected to cover would be 130 to 370 miles (within the extremes indicated).

There are of course a number of sources of error which might raise or lower these estimates. In all probability there was a delay in the recovery of the drift-bottles, which means that the rate of transport was somewhat greater than that computed. On the other hand, it is unlikely, in view of the amount of turbulence from wave action that the majority of the larvae are carried at as great a rate as that indicated by the drift-bottles. In that case the distances covered would be less than those computed.

However, since the nearest large stock of "offshore" lemon soles to that in Hecate Strait lies more than 550 miles to the southward (off the Washington coast), and hence well beyond the maximum range indicated above, it is reasonable to suppose that the young fish present along the shallows adjacent to Graham Island are mainly the progeny of the Hecate Strait stock.

In summary, evidence of current flow through Hecate Strait suggests that young lemon soles present along the Graham Island side of the Strait are carried there from some region to the south. This coincides with the observation from tagging that the direction of migration of spent fish in the spring is also from the south. Although there are a number of possible sources of error in the estimates of rate of drift of the larvae they tend to support the conclusion that the young fish present along the Graham Island shore are the progeny of Hecate Strait adults.

EVALUATION OF FLUCTUATIONS IN YEAR-CLASS STRENGTH

The study of variation in the strengths of lemon sole year-classes has been confined to data contained in samples from the commercial catch. It involves a ten-year period beginning in 1944.

SAMPLING OF THE CATCH

At frequent intervals throughout the season of the lemon sole fishery, samples of 200 to 300 fish were collected at random from the fillet lines at the main ports of landing, Prince Rupert and Vancouver. The total length of each fish was measured to the nearest centimetre and the sex determined. At the

same time the otolith from the sacculus of the ear on the blind (left) side was removed and stored.

The method of otolith collection used was a modification of that described by Blegvad (1927). A series of shell-vials were arranged in a number of rows of holes drilled in an "otolith board", in such a way that each vial represented a centimetre size group of each sex. When an otolith was removed from a fish it was then assigned to the vial marked for fish of that size. In this way all otoliths of fish of the same size and sex were accumulated in one vial. When the sampling of several hundred fish was completed the otoliths were removed from the vials, group by group and placed in a single storage vial. The groups were kept separate from one another by stiff paper dividers labelled with identifying serial numbers. Before storage, a clearing agent (glycerine and water solution containing thymol) was added to the sample vial.

Since samples were taken at a fairly uniform rate throughout the season each year, it was desirable to weight these roughly according to the seasonal trend in landing. This enabled the description of an average age composition of the commercial catch in each year.

During the spring months the area of operation of the main section of the fleet shifts northward from the Warrior grounds to the Two Peaks grounds. As has been shown in an earlier section, this shift in fishing effort is in response to a northward migration of the stock. Although considerable size and sex segregation takes place, particularly during the summer months, the fleet operates over a variety of depths and localities. Hence, it is presumed that the relative proportions of the age-groups landed which were free from the effects of size selection by the gear, were reasonably representative of those age-groups present on the fishing grounds.

For the sake of continuity it has been necessary to make some adjustment to account for a strike which occurred during the spring months of 1947 and which prevented sampling of the stock at that time of year. Since the age composition in samples taken in the fall of 1947 conformed with the trend indicated by 1946 and 1948 data, the fall records (October and November) have been used to represent the situation during the spring of that year. Admittedly, some error is introduced, since one would expect age-groups which are being recruited to the marketable population to be better represented in the fall (after the growing season) than in the spring. However, this error is not likely to be great, since only those age-groups which are more or less completely recruited are to be used in computations of relative year-class strength.

It has been considered desirable to treat only the data on female lemon soles, because of the pronounced differences between male and female fish in respect to their size and age composition in the catches. The male fish (amounting to less than 30% by numbers in the catch) have been rejected because of their slow growth and hence their tendency to slow recruitment.

ANNUAL FLUCTUATIONS IN SIZE COMPOSITION

The percentage length-frequency composition of female lemon soles caught in Hecate Strait in the years 1944-53 is presented in Figure 13 (data from

Appendix 1) according to the method developed by Sund (1930). For each year the distribution has been plotted in terms of the percentage deviation from the mean distribution for the years 1944-53, with the exclusion of the 1947 data.

It will be noted that during this period a recruitment of small fish, in greater strength than average, took place in the 1946 season and remained in evidence during the succeeding five years as it passed through the fishery. The remnants of an earlier "wave" of better than average recruitment are indicated in the 1944 to 1946 distributions. In 1951 there was a slight foreshadowing of another influx of exceptional recruitment, which appeared most strikingly in 1952. An explanation of these fluctuations and trends in size composition is to be found in data on age composition.

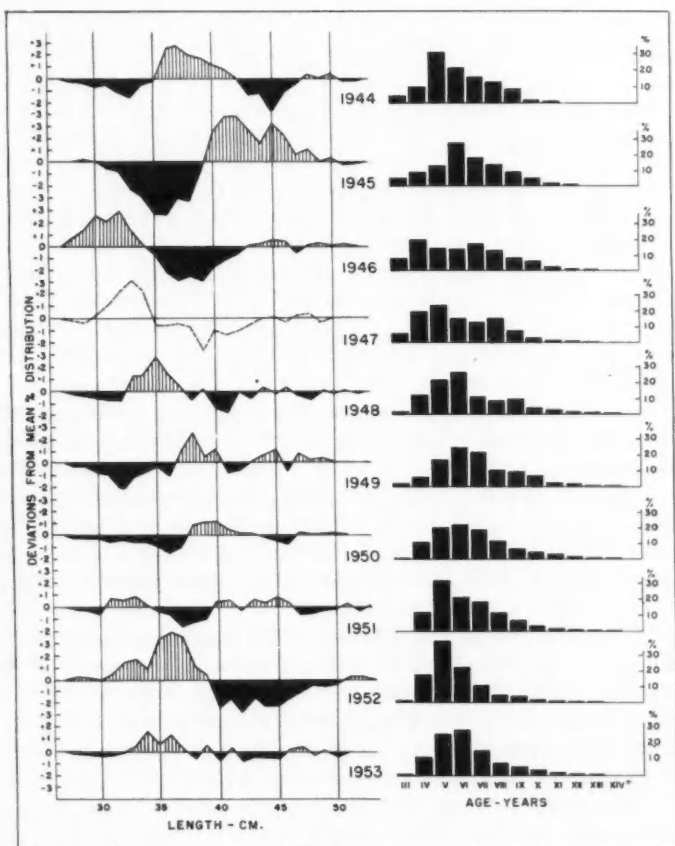


FIG. 13.—Length and age structure of female lemon soles in the Canadian catch from Hecate Strait. LEFT SIDE: Deviations of the length frequency from the 1944-53 mean, as percentage. RIGHT SIDE: Age composition, as percentage.

ANNUAL FLUCTUATIONS IN AGE COMPOSITION

The percentage age composition for the ten year period (data from Table IV) is illustrated in Figure 13, with the size composition data. It will be observed that the year-class of 1939 (appearing in 1944 as five-year-olds) remained in prominence for a period of three years. That of 1942 (appearing in 1946 as four year-olds) also predominated for a period of three years (1946-48). It is to be noted that the heavy influx of small fish in 1951 was apparently attributable to the 1947 year-class.

TABLE IV.—Percentage age composition in samples from the commercial catch of lemon sole from Hecate Strait.

Year of capture	Age in years													Numbers sampled
	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV+		
1944	3.6	9.5	26.0	21.6	15.8	13.1	8.6	1.4	0.5	0.0	0.0	0.0	250	
1945	4.8	8.2	12.6	26.6	17.8	13.6	9.0	4.9	1.5	0.2	0.0	0.0	846	
1946	7.5	19.2	13.9	13.1	16.7	12.5	8.0	5.7	2.1	0.6	0.3	0.0	2971	
1947	5.5	19.1	22.6	14.6	12.9	13.8	6.8	2.7	1.2	0.4	0.1	0.0	902	
1948	1.2	12.0	21.7	26.6	11.3	8.9	9.4	3.9	2.4	1.5	0.6	0.4	2429	
1949	0.0	6.0	16.2	24.3	20.5	10.6	9.8	6.5	2.6	2.0	0.7	0.3	1500	
1950	0.1	10.4	20.0	21.8	18.4	11.9	6.8	4.7	3.1	1.8	0.5	0.4	2673	
1951	0.0	11.5	26.1	20.8	17.8	11.4	6.5	3.1	1.4	0.7	0.1	0.1	2939	
1952	1.1	17.3	38.6	22.2	10.5	4.4	3.3	1.5	0.6	0.3	0.1	0.0	1435	
1953	0.1	11.4	25.7	28.2	15.4	7.7	5.5	3.4	1.5	0.8	0.4	0.0	2148	

QUANTITATIVE EXPRESSION OF BROOD STRENGTH

(a) METHOD

For many years investigators in European countries have been obtaining quantitative measurements of year-class strength of such species as haddock and plaice by annual systematic sampling of nursery grounds to determine the numbers of juvenile fish per unit of sampling gear (Thompson, 1929; Johansen 1927; Buckmann, 1936). Because of limitations of time and funds and a lack of knowledge (until very recently) of the distribution of the juvenile segments of the lemon sole population of Hecate Strait, this direct approach could not be attempted.

As an alternative, attention has been focused on the possibility of obtaining some index of relative abundance from the adult fish as they occur in the commercial catch. If neither fishing effort nor catchability (vulnerability of the fish to capture) fluctuate from year to year, then it is possible to assess abundance from the total annual catch of each age-group. Such an approach has been used in estimating strengths of pilchard year-classes (Walford, 1946). If fishing effort fluctuates, but catchability remains constant from year to year, then data on catch-per-unit-effort and age composition can be utilized to obtain these estimates. This approach has been used in evaluating herring fluctuations (Tester, 1948). Regarding the lemon sole data, fishing effort cannot be considered to have remained constant during the period of study. Furthermore, an inspection of the

figures on catch-per-hour in Table I and the age composition data in Figure 13, shows clearly that catchability is not a constant factor from year to year. The sharp changes in catch-per-hour between the years 1945 and 1946 and between 1949 and 1950 are in no way explained by the minor changes in age composition in those years. Thus any treatment embodying the assumption of constant catchability would likely introduce serious errors into the computations of relative year-class strength.

It remains therefore to consider a less precise method, namely, the contributions of a year-class in terms of its *percentage* contribution to the catch each year. In this case the basic assumption would be that population size, rather than catchability, remains constant from year to year. Clearly, this assumption is not strictly tenable, since Figure 13 shows that some fluctuation in the age composition (and hence, presumably in the size of the population) has been taking place. Added to this is the fact that there has been a general upward trend in catch during the period of study.

However, for a number of reasons it is believed that the assumption of constant population level is much less misleading than the assumption of constant catchability. In the first place, a considerable number of age-groups are involved in the catch each year. Thus the influence, on the year to year population level, of moderate fluctuations in size of year-classes being recruited to the marketable population would tend to be dampened. In the second place, since the experiment covered only a short period of years, the effect of a long-term trend in abundance is minimized. If there had been any radical change in abundance over the period of the experiment, this fact would have been manifest in the catch-per-unit of effort data of Table I. Although there was a trend in the catch during the period, the annual yield (with the exclusion of that of 1950) has been only a small segment of the total population. The average annual rate of exploitation between 1944 and 1951 has been estimated to be less than 16% (Ketchen, 1953).

Further support for the admissibility of the assumption of a constant population level and the utilization of percentage composition in computing an index of the relative strengths of year-classes has been obtained from simple population models. In a model in which the number of age-groups and the annual survival rate is approximately the same as that of the Hecate Strait lemon sole population, the amplitude of the fluctuations in year-class strength, whether it be small or moderately large, has no appreciable effect in forcing a departure of the trend in *percentage* values of year-classes from the *absolute* or *numerical* values.

A practical example which can be regarded as exhibiting the extreme effects is contained in data on herring (Tester, loc. cit.). The percentage of year-classes follow the absolute values in so far as the *order* of the fluctuations is concerned. They differ somewhat in their amplitudes and in their over-all trends.

(d) RESULTS

Since the period of study covers only ten years, there are not sufficient data to compute the percentage contribution of any one year-class throughout its entire existence in the fishery. In order to circumvent this difficulty and to make

use of as many year-classes as possible, the contributions of a year-class have been considered when it appeared in the fishery at ages five, six and seven, only. For example, the 1939 year-class contributed (as five-, six- and seven-year-olds) 26.0%, 26.6% and 16.7% of the numbers of fish caught in 1944, 1945 and 1946, respectively (Table IV). The three percentage contributions for this and other year-classes have been extracted from Table IV and summed in Table V.

TABLE V.—Percentage contributions of ten year-classes at ages five, six and seven years.

Age	Year class										Mean
	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	
V+	(21.4)	26.0	12.6	13.9	22.6	21.7	16.2	20.0	26.1	38.6	21.91
VI+	21.6	26.6	13.1	14.6	26.6	24.3	21.8	20.8	22.2	28.2	21.98
VII+	17.8	16.7	12.9	11.3	20.5	18.4	17.8	10.5	15.4	(25.1)	16.64
Total	60.8	69.3	38.6	39.8	69.7	64.4	55.8	51.3	63.7	91.9	60.53
Dev. from mean	+0.3	+8.8	-21.9	-20.7	+9.2	+3.9	-4.7	-9.2	+3.2	+31.4	

Use has been made of two year-classes for which complete data were not available, namely those of 1938 and 1947. The former appeared as five-year-olds in the fishery in the year before the study began and the latter (at the time of writing) had not yet appeared as seven-year-olds. Estimates of these missing contributions have been made on the basis of contributions in other years, in the following manner: from Table V it has been computed that the mean percentage of five-year-olds (1939-46, incl.) was 19.90%, that the mean of the six-year-olds in the same period was 21.25% and that of the seven-year-olds, 15.43%. Accord-

ingly, the mean ratio, $\frac{V}{VI + VII}$ is 0.542. An estimate of the contribution of the 1938 year-class when it appeared as five-year-olds is obtained by multiplying this ratio by the sum of the contributions of the 1938 year-class as six- and seven-year-olds, i.e. $0.542 (21.6 + 17.8) = 21.35\%$. A similar estimate of the contribution of the 1947 year-class as seven-year-olds is obtained by computing the mean ratio, $\frac{VII}{V + VI}$ for the period 1939-46, and multiplying this by the sum of the contributions of the year-class as five- and six-year-olds, namely $0.375 (38.6 + 28.2)$, which is equal to 25.05%. These two estimates have been incorporated in the totals and averages shown in Table V.

The totals shown in this table are to be used as indices of the relative magnitudes of the various year-classes. For convenience of future reference these figures are expressed as deviations from the mean value for the ten year-classes. It is evident that throughout the early history of the fishery for lemon soles in Hecate Strait (1944 to 1953) there have been substantial fluctuations in the strengths of contributing year-classes. Broods produced in 1938, 1939, 1942, 1943, 1946 and 1947 were apparently stronger than those produced in 1940, 1941, 1944 and 1945. Of particular note is the strength of the 1947 year-class and the weakness of the 1940 and 1941 year-classes.

At this point it is advantageous to draw together the results which have appeared in the various sections developed so far. In the first place, fluctuations in the strengths of a number of lemon sole year-classes have been revealed in age composition studies of the commercial catch from Hecate Strait. Secondly, there is evidence that the O-group fish which occur along the western side of the Strait eventually join the adult stock which is the object of the fishery along the eastern side. Furthermore, the evidence of prevailing water currents in Hecate Strait suggests that the O-group lemon soles originate from a region to the south of the nursery area. That this region lies somewhere in lower Hecate Strait or Queen Charlotte Sound is suggested by the pattern of movement of the adults (spawners) and is supported to some extent by evidence of the rate of drift of surface currents which carry the young northward through the Strait.

Assuming that the size of a lemon sole year-class is determined during the pelagic stage, the key to the observed fluctuations in survival lies in what transpires in the region of the Strait lying between the proposed spawning area and the nursery grounds of Graham Island. The problem now is to determine those environmental factors which are likely to have a bearing on the success of the translocation of the eggs and larvae between these two regions.

ENVIRONMENTAL FACTORS INFLUENCING SURVIVAL

THE CRITICAL PERIOD

Before considering the physical data on the environment it is important to define the time of year when the fate of a lemon sole year-class is determined. The principle is now fairly generally established that the period of high and variable mortality in marine fishes occurs at a very early stage in the life-history (Hjort, 1914, 1926; Graham, 1930; Thompson, 1930; Poulsen, 1930; Russell, 1942). For present purposes the critical period for the lemon sole is considered to be the interval when the young are in the pelagic stage. As mentioned earlier, this stage is believed to occupy a period of six to ten weeks, sometime in the first three or four months of the year.

To judge from conditions in the Strait of Georgia, spawning begins late in December, reaches a peak about the middle of February and is completed late in March or early April. On the assumption of a six- to ten-week pelagic stage, the peak abundance of pelagic young would occur from approximately the middle of February to sometime during the month of April. This schedule may be expected to vary slightly from year to year as the result of variations in the period of peak spawning.

Of course, the application of information on events in the Strait of Georgia to Hecate Strait must be treated with caution. Certainly, in other flatfish species (e.g. the plaice and flounder of the North Sea) there is considerable variation from area to area in the period of peak spawning (McIntosh and Masterman, 1897). Yet it is apparent from the comparison of the size compositions of young O-group fish between the two areas for a given time period, that the peak spawning periods are not radically different. Sampling in 1954 suggested that the peak

spawning took place no more than a week or two ahead of that in the Strait of Georgia.

In order to give ample consideration to possible differences in the period and duration of the pelagic stage in the two areas, it is desirable to assign rather broad time limits for preliminary investigation of the factors influencing survival. It is presumed for the present that the peak of the pelagic stage, namely the period when the majority of the larvae are adrift, occurs sometime within the period January to April, inclusive.

SOURCE AND ADEQUACY OF HYDROGRAPHIC INFORMATION

Hydrographic information on Hecate Strait for the period of years under consideration is limited to observations made at various lighthouse stations around its perimeter. As part of the program of the Pacific Oceanographic Group, these stations collect daily records of temperature and salinity at the sea surface. Data which are to be considered have been obtained from four positions—Triple Island, Ivory Island, Pine Island and Cape St. James (see Fig. 2).

(a) WATER TEMPERATURE DATA

Since the four stations register the same order of change in temperature conditions from year to year (Fig. 14) it is permissible, for the sake of simplicity, to focus attention on the records of one station. Although Cape St. James is the nearest station to the proposed spawning area, the records which can be judged to be reliable involve only the years since 1942. Thus they do not cover the period for which there are biological data on lemon sole fluctuations (1938 to 1947). The Pine Island station provides records for the required period, but its distance from the so-called critical area in Hecate Strait, makes consideration undesirable. The records from Ivory Island also cover the period since 1938, but

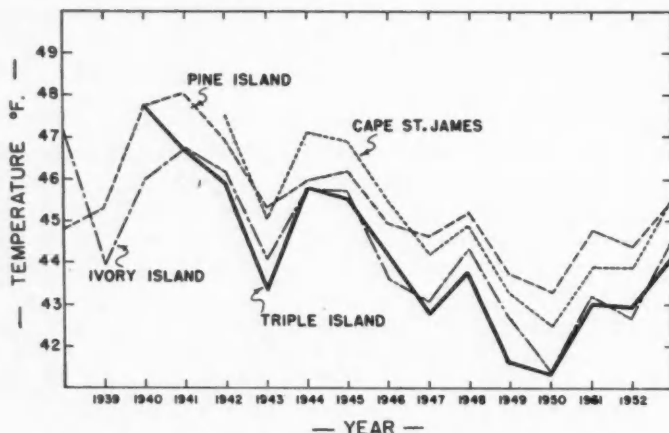


FIG. 14.—Trends in the mean temperature of the sea surface (January–April, inclusive) at four lighthouse stations in the vicinity of Hecate Strait.

this station is not exposed to the weather conditions prevalent in the open Strait. Since there will be need for study of wind as well as water conditions, the use of this station is not desirable. The choice falls then on Triple Island, a station which lies 30 to 60 miles from the Graham Island nursery area. Since this station is an exposed position adjacent to the narrowest section of Hecate Strait, it seems to hold greater possibilities than the others, as a monitor of water and weather conditions in the area under consideration.

Records from the Triple Island station have been collected only since 1940. Hence it is necessary to make estimates on the basis of records at other stations for the missing years of 1938 and 1939. That such an extrapolation would not lead to large error, is reasonable in view of the close similarity of the trend at all four stations. Calculation of the mean monthly temperature at Triple Island for the periods, December 1937 to May 1938 and December 1938 to May 1939, has been made on the basis of the relation between the *average* of conditions at Pine Island and Ivory Island, and those at Triple Island in more recent years. The estimated temperatures appear in brackets in Table VI. Included in Table VI are five series of mean temperatures obtained from two-month combinations of monthly means and four series obtained from three-month combinations of monthly means. The purpose of these will be apparent presently.

It might be argued that surface water temperatures are not representative of conditions in the environment of the pelagic eggs and larvae of the lemon sole, particularly if they are not confined strictly to the surface of the sea. However, various sources of information support the view that the wide variations in surface temperature as shown in Figure 14 are representative of conditions over a wide range of depths. Bathythermograph traces for the first quarter of the year show virtually isothermal conditions in Hecate Strait. This is to be expected in view of the wind intensity and the shallowness of the sea. The differences shown in Figure 14 for the period 1938 to 1942 compare well with those recorded in surveys by the International Pacific Halibut Commission. Van Cleve and Seymour (1953) show that the differences were maintained to depths of well over 100 metres.

(b) SALINITY DATA

Unlike the records of water temperature, those of surface salinity for the various stations around Hecate Strait bear little resemblance to one another (Fig. 15). This is to be expected in view of the difference at these locations in the influence of freshwater run-off from the land. Relatively high salinities are registered at Cape St. James, which is classed as an oceanic station and is remote from freshwater influence, whereas relatively low salinities are recorded at the coastal station of Ivory Island. Neither are considered to be typical of conditions within Hecate Strait. Salinities at Triple Island are intermediate to those at Cape St. James and Ivory Island, but the representativeness even of this station is suspect in view of its proximity to sources of freshwater.

The annual cycle of salinity of Triple Island coincides with the cycle of run-off from the Skeena River (Pickard and McLeod, 1953). That this relation-

TABLE VI. One-, two- and three-month mean temperatures of the sea surface at Triple Island, British Columbia.

Period	Temperature (°F.)													
	1937-38	1938-39	1939-40	1940-41	1941-42	1942-43	1943-44	1944-45	1945-46	1946-47	Mean			
December	(48.9)	(45.4)	48.4	48.7	47.8	45.8	47.6	47.9	44.7	43.5	46.87			
January	(47.9)	(46.1)	48.0	47.5	46.3	43.2	46.7	47.1	44.2	41.8	45.88			
February	(44.2)	(43.0)	47.3	45.9	46.2	43.0	45.5	45.5	43.6	41.9	44.61			
March	(45.2)	(43.1)	47.3	46.0	45.2	42.7	44.3	44.7	44.1	43.1	44.57			
April	(45.7)	(44.0)	48.7	47.5	46.3	44.2	45.4	45.0	44.6	44.4	45.58			
May	(48.8)	(47.8)	51.5	49.8	48.9	47.2	47.4	48.2	48.4	47.3	48.53			
Dec.-Jan.	(48.4)	(45.7)	48.2	48.1	47.1	44.5	47.2	47.5	44.5	42.6	46.38			
Jan.-Feb.	(46.0)	(44.5)	47.6	46.7	46.2	43.1	46.1	46.3	43.9	41.8	45.22			
Feb.-Mar.	(44.7)	(43.0)	47.3	46.0	45.7	42.8	44.9	45.1	43.8	42.5	44.58			
Mar.-Apr.	(45.5)	(43.5)	48.0	46.8	45.7	43.4	44.9	44.9	44.3	48.7	45.57			
Apr.-May	(47.3)	(45.9)	50.1	48.7	47.6	45.7	46.4	46.6	46.5	45.8	47.06			
Dec.-Feb.	(47.0)	(44.8)	47.9	47.4	46.8	44.0	46.6	46.8	44.2	42.4	45.79			
Jan.-Mar.	(45.8)	(44.1)	47.5	46.5	45.9	43.0	45.5	45.8	44.0	42.3	45.04			
Feb.-Apr.	(45.0)	(43.4)	47.8	46.5	45.9	43.3	45.1	45.1	44.1	43.1	44.93			
Mar.-May	(46.6)	(45.0)	49.2	47.8	46.8	44.7	45.7	46.0	45.7	44.9	46.24			

ship exists even during the early part of the year when the run-off is at a minimum is suggested by a low negative correlation between surface salinity and water temperature at that station (January–April period from 1940 to 1951). It is improbable that any such relationship exists in the open water of Hecate Strait where the influence of the Skeena River is known to be negligible even during periods of normal run-off (Cameron, 1948). Thus, there is little, if any, basis for considering the relationship of annual changes in salinity at Triple Island to the observed changes in year-class strength of the lemon sole.

At any rate, the annual variations in surface salinity in the open water (Fig. 15) are of very small order, and hence it is reasonable to suppose that this factor can be ruled out as having any strong bearing on lemon sole survival. At Cape St. James the range of variation over ten years in the January–April period was only 0.42‰, while that at Pine Island and Triple Island was 0.61‰ and 0.58‰ respectively. Since these are strictly surface measurements they probably indicate the maximum variation which occurred in the upper layers of the sea.

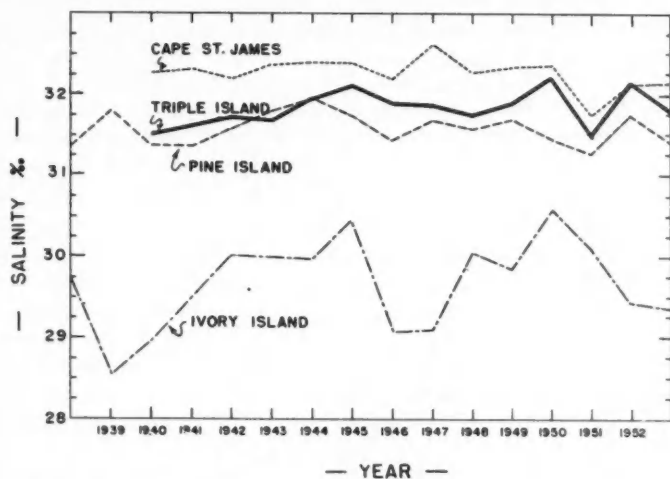


FIG. 15.—Trends in the mean salinity of the sea surface (January–April, inclusive), at four lighthouse stations in the vicinity of Hecate Strait.

TEMPERATURE AND ITS RELATION TO BROOD STRENGTH

Water temperature data have been examined for a number of intervals and combinations of intervals during the broad period which is likely to be of significance to survival. Although, as mentioned previously, the peak of the pelagic stage probably occurs within the January to April period, it is desirable to take some account of the fact that spawning may begin as early as December and that the progeny of late spawning may be adrift well into the month of May. Accordingly, consideration has been given to two- and three-month intervals within the December to May period.

(a) TWO-MONTH INTERVALS

Tests of correlation have been made between the strengths of ten year-classes (Table V) and the mean temperature conditions over five two-month intervals in the ten years when the broods were produced (i.e., Dec.-Jan., Jan.-Feb., Feb.-Mar., Mar.-Apr., and Apr.-May as shown in Table VI). The results show an *inverse* relationship in all five cases (Table VII). All correlation coefficients are statistically significant at the 5% level and 3 are significant at the 1% level of confidence.

TABLE VII.—Correlation (r) between strengths of ten year-classes and the mean temperature of the sea surface during two- and three-month intervals.

Interval	r	Interval	r
Dec.-Jan.	-0.795	Dec.-Feb.	-0.826
Jan.-Feb.	-0.864	Jan.-Mar.	-0.904
Feb.-Mar.	-0.797	Feb.-Apr.	-0.792
Mar.-Apr.	-0.715	Mar.-May	-0.696
Apr.-May	-0.706

(b) THREE-MONTH INTERVALS

Similar tests of correlation have been made between the strengths of the ten year-classes and mean water temperature for three-month intervals. The

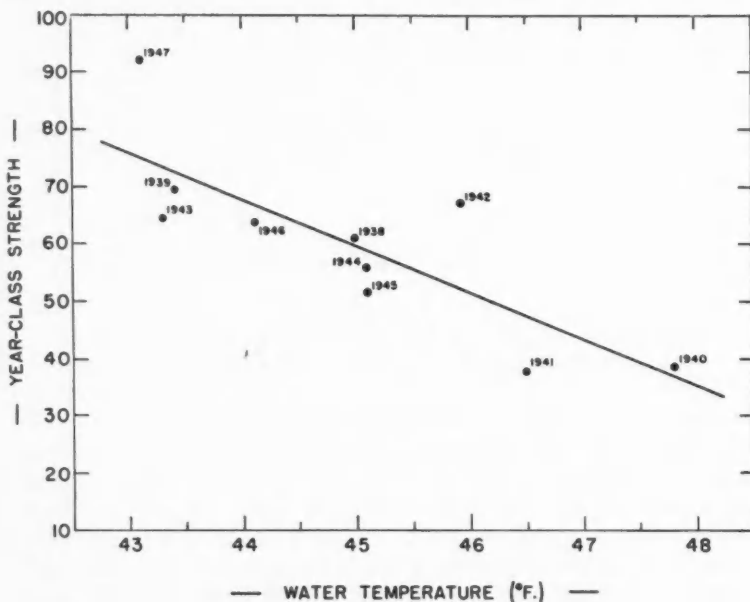


FIG. 16.—Year-class strength of the lemon sole and its relation to water temperature at the approximate time of the pelagic stage (February–April, inclusive).

results are shown in Table VII also. All correlation coefficients are statistically significant at the 5% level of confidence and three are significant at the 1% level.

It must be emphasized that the occurrence of the highest correlations in the two-month period of January–February and in the three-month period of January–March does not necessarily mean that those intervals mark the critical period for the lemon sole. The difference between the lowest and highest values of r shown for the two-month periods is not statistically significant. In the case of the three-month correlations there is a statistically significant difference between only the lowest and highest values of r . All that can be said is that statistically significant correlations exist for the intervals within the broad period when the pelagic stage of the lemon sole is believed to occur.

For the purpose of illustration the strengths of the ten year-classes (Y) have been plotted against average water temperatures (X) for the February–April period (Fig. 16). The equation of the line of best fit is $Y = 425.5 - 8.1 X$.

EXPLANATION OF THE RELATION BETWEEN TEMPERATURE AND BROOD STRENGTH

The problem now arises of finding an explanation for the observation that better than average survival occurs in years when water temperatures are below average. It is important to discover whether temperature is involved directly or whether it is merely associated with the causal factor(s).

(c) TEMPERATURE AS A LETHAL FACTOR

The fact that relatively weak year-classes are produced in years when the water temperature is high might suggest that at higher levels temperature operates as a lethal factor. If the lemon sole were a species whose centre of distribution lay in Arctic waters such a possibility would be worthy of consideration. However, the species is distributed in abundance far to the south of Hecate Strait in regions where the winter temperatures of the surface waters are considerably higher than those in the Strait. For example, adjacent to San Francisco, where the annual catch amounts to several million pounds, the mean surface temperature for February is 6° to 8°F. higher than the highest experienced in Hecate Strait.

(d) TEMPERATURE AS A CONTROLLING FACTOR

Dannevig (1894) and Johansen and Krogh (1914) have shown that temperature determines the rate of embryological development and the time of hatching of flatfishes. Thus, temperature may govern the strength of a year-class by retarding or accelerating the rate of growth during the pelagic stage to such an extent that it affects radically the duration of that stage. The duration in turn would determine the extent of influence of currents and hence the dispersal to suitable nursery grounds. Low temperatures would promote slower growth, a longer pelagic stage and a greater distance of drift, than would high temperatures.

Some indication of the magnitude of temperature influence has been obtained from a laboratory experiment designed to determine the rate of embryological growth to hatching at various temperatures.

METHOD. Jars of seawater, each containing several hundred newly fertilized lemon sole eggs, were placed in a number of water baths maintained at various temperatures. The mean temperature values and the temperature ranges in each of eight tanks throughout the period of the experiment are given in Table VIII. Unfortunately, because of a lack of suitable control equipment in four of the tanks (nos. 2, 3, 4 and 6) there was considerable overlapping of the temperature ranges.

TABLE VIII.—Tank temperatures in the experiment on the rearing of lemon sole eggs.

Tank Number	Mean temperature °F.	Range of temperatures °F.
1	50.5	50.0–51.0
2	47.0	46.0–47.5
3	45.8	44.5–47.2
4	44.7	43.5–45.5
5	40.0	39.7–40.5
6	38.9	37.1–39.1
7	37.8	37.6–38.0
8	36.7	35.0–37.0

Since it was found that egg mortality from causes other than temperature (fungal infection) proceeded at a rate which tended to leave only a few eggs alive at the time of hatching, it was necessary to set up a system of observation of rates of growth which would permit some estimation of the "modal" time to hatching. By frequent sampling of the eggs it was possible to classify them according to a number of stages in the course of their development. Some of the prominent features described by Budd (1940) in his work on the embryology of the lemon sole have been used in standardizing the classification. Supplementary information on flatfish embryology has been obtained from the work of Orcutt (1950) on the starry flounder.

Stages which have been used as standards in the development of the lemon sole egg are as follows:

- Stage 0: Time of fertilization.
- Stage 1: Appearance of the blastodermal cap.
- Stage 2: Early germ ring.
- Stage 3: Intermediate germ ring.
- Stage 4: Closing of the blastopore (and appearance of Kupffer's vesicle).
- Stage 5: Formation of the tail bud.
- Stage 6: Appearance of heavy pigmentation.
- Stage 7: Pulsation of the heart (and occasional body movement).
- Stage 8: Hatching.

Stages 1 to 8 are illustrated diagrammatically in Figure 17 and photographs of some of the stages are shown in Figure 18.

It is realized that errors in the timing of a stage of development must have occurred, since the eggs were not under constant observation and since the

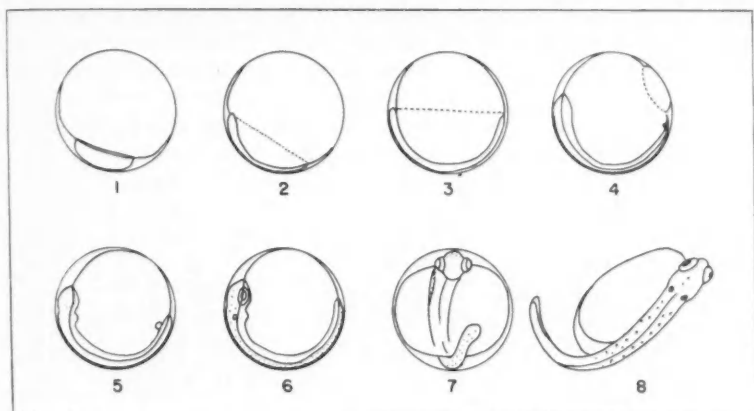


FIG. 17.—Diagrammatic representation of stages in the development of the lemon sole embryo.

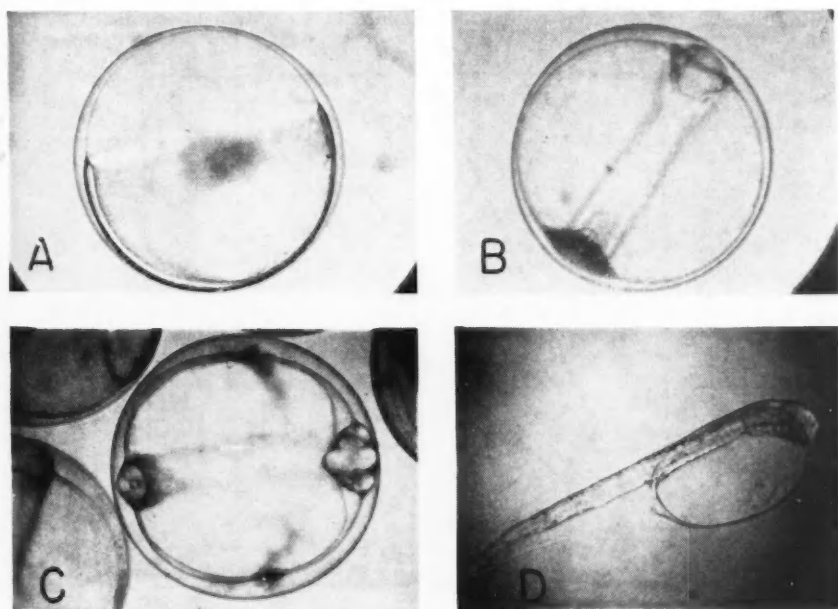


FIG. 18.—Photographs of certain stages in the development of the lemon sole embryo showing (A) migrating germ ring, intermediate to stages 3 and 4, (B) late stage 4, (C) stage 6 and (D) newly hatched larva.

stages (particularly of later development) did not lend themselves to precise definition. In earlier stages where the structural changes occur more rapidly, it was possible to note steps in the development which were intermediate to those outlined above.

RESULTS. In presenting the results, use has been made of a graphical method used by Worley (1933) in the study of mackerel development and later by Bonnet (1939) in the study of cod egg development. In Figure 19 the various stages are plotted on the vertical axis. Because they were chosen on the basis of certainty of recognition, they are not equally spaced. These points have been chosen in such a way that the data of Budd (loc. cit.), on the rate of development at 55.4°F., approximate a straight line (solid line in Fig. 19). The results obtained in the present experiment at the various temperatures listed in Table VIII were then plotted against the same ordinates. Straight lines have been fitted by least squares to obtain estimates of the modal time to hatching in those cases where there were sufficient points to detect a trend.

In three tests (at temperatures of 36.7°, 37.8°, and 38.9°F.) no success was achieved in rearing the eggs. In all cases complete mortality apparently occurred before development had passed the formation of the blastodisc or the first cleavage. In two tests (40.0° and 44.7°F.) the eggs proceeded to develop but succumbed before they reached the hatching stage. The regression line of the latter can be extrapolated with some confidence to obtain an estimate of the

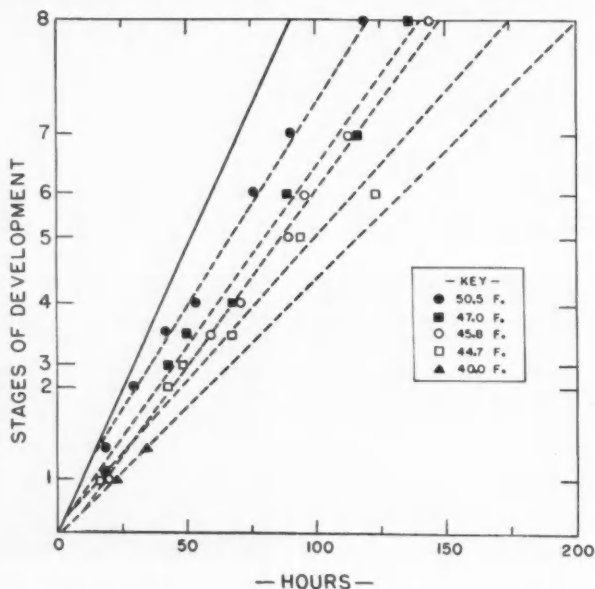


FIG. 19.—Development of the lemon sole egg at various temperatures.

time which would have been required to reach the hatching stage. That of the former is of questionable accuracy because of the length of the extrapolation.

Krogh (1914) showed that in various marine fish embryos the rate of development, when plotted against temperature, gives a straight line, that is the relationship conforms to the intercept formula

$$v = k_0 + k_1 T$$

where v is the velocity or rate (100 times the reciprocal of y , the days from fertilization to hatching), T is the temperature in degrees Centigrade and k_0 and k_1 are respectively the intercept and slope constants. Using the data from Figure 19 a velocity curve has been plotted in Figure 20 and compared with those presented by Krogh for two European flatfishes, the flounder (*Pleuronectes flesus*) and the plaice (*P. platessa*). The straight line relationship indicates that the increase in rate is in simple proportion to the increase in temperature, within the range of temperatures considered. The equation for this line is

$$v = 2.05T - 0.27$$

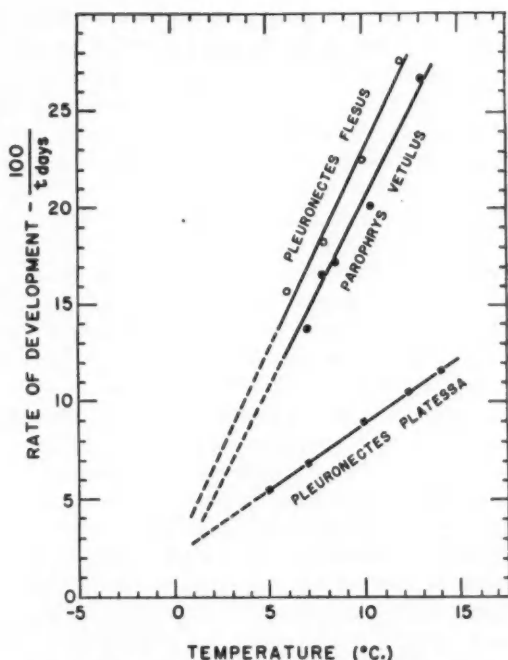


FIG. 20.—The relation of temperature to the rate of development to hatching of lemon sole (*Parophrys vetulus*), as compared with two European flatfishes (after Krogh, 1914).

TEMPERATURE AND THE DURATION OF THE PELAGIC STAGE. Consider now the possible influence on the pelagic stage of the lemon sole of the various temperature conditions experienced in the years 1938 to 1947. The highest mean temperature for the Feb.-Apr. period occurred in 1940, namely 47.8°F., (see Table VI) while the lowest mean temperature occurred in 1947 (43.1°F.). Estimates of the number of days to hatching under such conditions are obtainable from the above equation.⁴

At 47.8°F. the time to hatching is estimated to be 5.6 days and at 43.1°F., 8.0 days. Thus, in 5.6 days the eggs developing at 47.8°F. might be expected to be 2.4 days ahead of those developing at 43.1°F. Assuming that this difference in rate of development is maintained throughout subsequent stages up to metamorphosis, one would conclude that, at the end of the pelagic stage (say eight weeks or 56 days) the larvae experiencing the higher temperature would be $\frac{56}{5.6} \times 2.4$ or 24 days ahead of those at the lower temperature. In other words, one might expect a 24-day difference in the pelagic stage, or a 24-day difference in the amount of time during which the young could be influenced in their distribution by the ocean currents.

The magnitude of the difference in the influence by the currents, of course, would be dependent on the velocity of the currents (i.e. the daily net transport). If the information extracted from the drift-bottle experiments concerning the rate of drift in Hecate Strait is not greatly in error, then such a difference would have a substantial effect on the distribution of the larvae. Assuming that the net drift is approximately four miles per day and that it is relatively constant from year to year, it follows that the drift of the young would be about 90 to 100 miles farther northward under conditions of relatively low water temperature than under those of relatively high temperature. Since the rearing area along the east coast of Graham Island is little more than 60 miles long, it is conceivable that relatively small differences in the average distance of drift each year would have considerable bearing on the numbers of young which are brought in contact with the shallow water. The fact that there is an inverse correlation between year-class strength and water temperature suggests that survival is better when there is a prolonged pelagic stage than when there is a short one. If the drift of Hecate Strait water follows a simple south to north pattern, this means that in years when the water temperature is high the young are prepared to go to the bottom before they reach the favourable rearing grounds in the northern part of the Strait. In years when the water is cold more larvae reach the rearing area.

Unless there is some current system within the broad northward pattern of drift which directs the water towards the Graham Island shore, or unless the spawning ground lies directly in the path of those currents which sweep along the western side of the Strait, it is unlikely that all the larvae which reach the

⁴Converting to Centigrade scale these temperatures are 8.8°C. and 6.2°C., respectively. The corresponding values for v are 17.8 and 12.4. Estimates of the number of days to hatching (t) are then obtained from the equation $t = \frac{100}{v}$.

northern part of the Strait would be in the vicinity of the restricted band of shallow water. Presumably there is considerable scattering of the eggs and larvae, much like that shown for the plaice of the North Sea (Buchanan-Wollaston, 1926) as a result of the variation in the direction and velocity of the currents at different depths. There is little likelihood that the larvae which are carried along the eastern side of the Strait would find suitable conditions for survival. Davis (1925) considered that the "hit or miss" method of dispersal of young by currents, accounts for the enormous fluctuations from year to year of invertebrate fauna which are narrowly restricted in their habitat on the Dogger Bank. A similar situation could be considered in the case of the lemon sole in Hecate Strait.

(e) TEMPERATURE AND RATE OF DRIFT

The variation in water temperature as depicted in Figure 14 is presumably related to variations in late-winter weather conditions adjacent to the British Columbia coast. There is a possibility, therefore, that the observed relationship between water temperature and brood strength is an indirect one, and that the causal connection is actually between wind induced current (direction and rate of drift) and brood strength. Unfortunately, this possibility is difficult to examine, in view of the limited value of existing data on wind conditions in Hecate Strait. Wind, like salinity, is a local phenomenon. In Hecate Strait the various wind recording stations are close to land and hence are not likely to provide a representative picture of conditions in exposed regions.

The northwesterly drift along the British Columbia coast as indicated by drift-bottle experiments (Fig. 12) apparently is the result of the south-easterly winds prevailing during the early months of the year. Yearly variations in the resultant effect of winds promoting a northward drift and winds promoting a southward drift through Hecate Strait might be expected to have some bearing on the efficiency of transport of eggs and larvae to the rearing area. Wind data from Triple Island and Dead Tree Point on the Queen Charlotte Islands show little, if any, similarity. At the former station there is a slight indication of a negative correlation between wind resultant and water temperature. No relationship is apparent at the latter station, and in neither case is there a clear relation between wind resultant and brood strength.

(f) BIOLOGICAL FACTORS ASSOCIATED WITH WATER TEMPERATURE

In the absence of direct evidence of biological factors or knowledge of their relationships to physical conditions in Hecate Strait, one can only speculate as to their importance in the observed fluctuations in survival. Two factors which might be associated with temperature and might play a prominent role in survival are the abundance of food and the abundance of predators present during the pelagic stage of the lemon sole.

In the sea, the production of the primary food supply (phytoplankton) is limited mainly by the availability of nutrient salts, the availability of light for photosynthesis and by the temperature of the water. Fluctuations in the influence of these factors from year to year, presumably would bring about fluctuations in

the density of the food supply for zooplankton and pelagic fish larvae (Johansen, 1927; Walford, 1946).

There is little to suggest, from physical data for Hecate Strait, that conditions were more favourable for the production of phytoplankton in years of good lemon sole production than in poor ones. Not only were water temperatures below average but so also was the amount of illumination. For the February–April period in the years 1938 to 1947 there was a negative correlation (-0.528) between year-class strength and the amount of sunlight, as registered at Prince Rupert.

If plankton production were higher in years when water temperatures were above average, the inverse correlation between temperature and year-class strength might be an indication of the effects of predation. In years of high phytoplankton production one might expect to find a high production of those small animals in the food chain which are immediately dependent on the phytoplankton. Plankton grazers, which include varieties of pelagic crustaceans, coelenterates, larval stages of benthic invertebrates, etc., have been demonstrated by numerous authors to be capable of diminishing materially the phytoplankton (diatom) populations (Sverdrup *et al.*, 1946: 772). Lebour (1923) has shown that a considerable variety of plankton grazers such as Ctenophora, Scyphozoa, pelagic annelids and chaetognaths, feed also on flatfish eggs and larvae. Thus, if a population of phytoplankton is capable of being diminished by grazers, a population of flatfish embryos and larvae might be similarly affected. However, as mentioned above these are merely speculations, and until such time when direct observations can be made, they cannot be properly evaluated.

LIMITATIONS OF THE TEMPERATURE–SURVIVAL CORRELATION

As Fisher (1950) points out, “if we choose a group of phenomena with no antecedent knowledge of the causation or absence of causation among them, then the calculation of correlation coefficients, total or partial, will not advance us a step towards evaluating the importance of the causes at work”. This point has been raised also by Widrig (1953) in his review of the investigations by Carruthers *et al.* (1951a, b).

In projects designed to relate changes in survival to phenomena in the natural environment, there is an almost inevitable lack of direct knowledge respecting factors which may play a role in survival. The collection of such information *before* the correlation is attempted, is usually prohibited by financial limitations, particularly in so far as marine investigations are concerned. To determine by direct observation the fluctuations in the pattern of dispersal of lemon sole eggs and larvae under various temperature conditions would be a prodigious undertaking. Nevertheless, such a project is desirable before full reliance can be placed on the conclusion concerning the observed relation between survival and temperature.

A few words should be said about the significance of correlation coefficients. In the absence of antecedent knowledge of the factors which influence survival, an investigator might explore a great variety of relationships before arriving at

one which is statistically satisfying. In such a case the probability value showing the statistical significance of a correlation can have little meaning, unless of course, the intensity of the search for correlation (number of trials) is adequately accounted for in the analysis. Just how account is to be taken of the number of correlation failures is not clear, for it is obvious that the number and order of trials may be a matter of personal judgement and hence undefinable in rules of analysis. The probability of correlations arising by chance alone, as pointed out by Gulland (1953), becomes even more difficult to evaluate when dealing with correlations based on much-adjusted data, and particularly with those based on relationships which depart from simple linearity.

The real test of the interdependence of two variables (brood strength and environmental factor) lies in the success with which the relationship enables prediction of future events.

In the case of the lemon sole research, it has been emphasized that fluctuations in year-class strength are related to temperature conditions over a wide area of Hecate Strait and over a wide range of time intervals. Thus, there is little basis for criticism that the correlation is precariously established on finely selected data, beyond that which is logically based on biological information. Further support for the trueness of the relationship is evident in the fact that it has survived fairly well the test of predicting three year-classes (1945-47) before they entered the fishery.

The relationship between temperature and year-class strength has been described as linear (Fig. 16) within the range of temperatures considered, namely 43° to 48°F. To what extent is the association likely to apply beyond this range? Little can be said about the upper limit, but information derived from the laboratory experiment on the rearing of eggs strongly suggests that at some point below 43°F. a linear, negative correlation ceases to exist. Very low temperatures could either have a lethal effect on the young, or so reduce the rate of growth (increase the length of the pelagic stage) that the young would be swept beyond the northern limits of the rearing ground. In other words, there must be an optimum temperature for survival either at or below 43°F.

It will be recalled from results of the laboratory experiment that all attempts to rear lemon sole eggs at temperatures of 38.9°F. or less, met with failure. Although eggs appeared to develop successfully at 40.0°F., there was insufficient control over the experiment to determine whether this temperature was in the vicinity of the lower incipient lethal level (defined as the temperature below which 50% of the population cannot live for an indefinite period of time; cf. Fry, 1947). All that can be said is that this level lies at some temperature above 38.9°F. and presumably below 43°F.—assuming of course that the relationship within the range of 43°F. and 48°F. really is linear.

As shown in Figure 14, in two years subsequent to the period of study (i.e. 1949 and 1950) water temperatures descended lower than at any time in the preceding eleven years. If the effects of a lower incipient lethal level became operative in those years, then one would expect a lower year-class value than that which could be predicted from the trend in Figure 16. Whether or not this

occurred in 1949 and 1950 cannot be determined until the broods produced in those years have made their contributions to the fishery.

There is a suggestion that the lethal effect of temperature in the vicinity of 39°–40°F. is a barrier to the northward distribution of the lemon sole in the northeast Pacific. Results of surveys conducted by the United States Fish and Wildlife Service (Ellson *et al.*, 1940, 1950; King, 1949, and Wigutoff and Carlson, 1950) suggest that the northern limit of the lemon sole's range is in the vicinity of Kodiak Island in the Gulf of Alaska. Data presented by Thompson and Van Cleve (1936: p. 42) show that winter sea surface temperatures in this area approximate those observed in laboratory experiments to be unfavourable for the survival of eggs.

SUMMARY

The lemon "sole" (*Parophrys vetulus*), a pleuronectid flatfish inhabiting the waters of Hecate Strait, British Columbia, is subject to fluctuations in the strengths of its year-classes. These fluctuations are related to water temperature conditions at the time of the pelagic stage. It is believed that water temperature governs the pattern of dispersal of the young to their rearing ground.

The lemon sole inhabits shallow sandy regions of the coast during the first year of its life. In Hecate Strait, suitable nursery grounds exist only along the east coast of Graham Island in the northern part of the Strait. Since spawning does not occur in the immediate vicinity of the nursery ground, the pelagic fry must be transported by currents to that region.

On the assumption that the fate of a year-class is determined early in the life-history (during the pelagic stage), it has been concluded that survival depends on events which transpire during the transport of young to the Graham Island rearing area. The pattern of migration of adult fish, as determined from tagging experiments, suggests that the main spawning area lies in southern Hecate Strait or Queen Charlotte Sound. Evidence of a northward current that would transport the larvae to the rearing area is provided from experiments with drift-bottles (conducted by the International Pacific Halibut Commission).

A strong inverse correlation has been found between year-class strength of the lemon sole and the temperature of the surface waters during the time of year when the pelagic stage occurs. Low temperatures, through their influence on growth rate, prolong the pelagic stage. Hence, in years when temperatures are below average, the larvae are carried for a longer period by the northward moving currents. This, it is believed, results in a greater deposition of young on the rearing grounds. Conversely, in years when temperatures are above average, the pelagic stage is of relatively short duration and the deposition of young is less.

Although water temperatures below 39°F. are lethal to lemon sole eggs, there is no evidence that this factor has played an important role in the fluctuations in survival of lemon sole year-classes hatched within the period of study (1938 to 1947).

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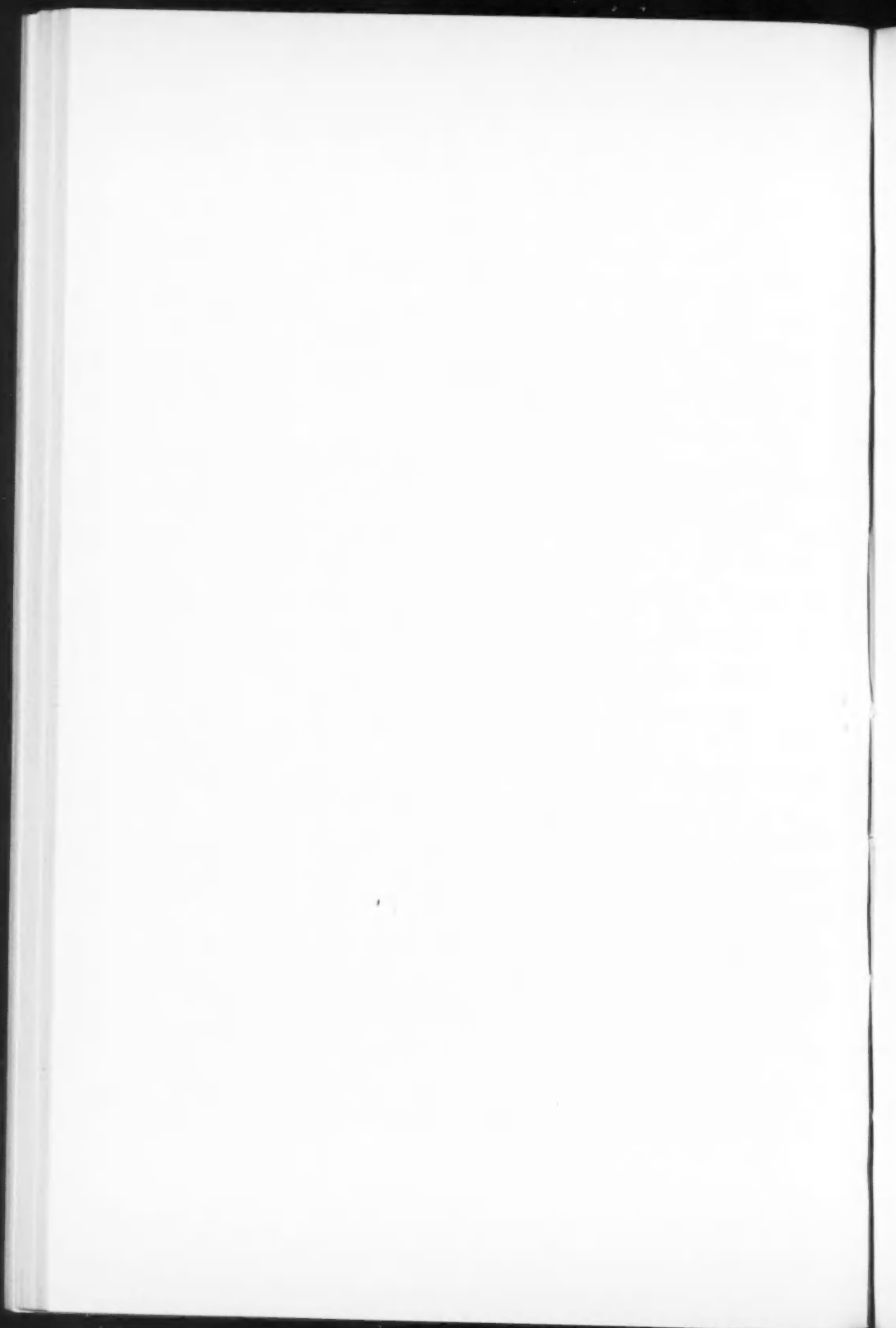
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APPENDIX 1. Length-frequency distribution of female lemon soles sampled from the commercial catch in Hecate Strait, British Columbia.

Length (cm.)	Per cent frequency										
	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	Mean ^a
28	0.0	0.1	1.0	0.2	0.0	0.0	0.0	0.0	0.6	0.0	0.2
29	0.0	0.4	1.7	0.1	0.0	0.0	0.1	0.1	0.8	0.1	0.3
30	0.0	0.7	3.4	0.4	0.2	0.0	0.5	0.3	1.5	0.3	0.7
31	0.8	0.9	3.4	1.4	0.6	0.4	0.8	2.1	3.2	1.0	1.3
32	1.6	1.9	5.7	3.8	2.0	0.6	2.4	3.3	5.2	2.6	2.7
33	2.4	1.8	5.3	6.7	5.3	3.0	3.5	4.9	7.2	4.4	4.0
34	4.9	2.4	5.4	7.7	6.8	4.4	4.8	5.6	7.5	6.9	5.3
35	7.3	3.3	6.9	9.9	10.4	7.2	6.6	7.2	11.4	7.9	7.5
36	10.5	3.6	5.8	8.1	9.3	6.9	6.5	7.4	10.3	9.3	7.9
37	11.5	5.9	6.0	8.6	9.2	9.9	7.8	7.3	12.0	8.9	8.8
38	11.5	6.3	7.1	9.0	8.8	12.2	10.5	8.4	9.6	9.1	9.5
39	10.5	8.1	5.8	7.8	8.5	9.3	9.8	7.8	7.7	9.2	8.7
40	9.7	11.3	7.0	6.4	7.2	9.8	9.7	9.1	5.6	7.8	8.6
41	8.1	10.1	6.2	6.0	5.3	6.5	7.6	7.9	5.4	7.6	7.2
42	6.5	10.3	6.0	5.3	6.4	5.9	6.5	6.3	3.1	5.6	6.4
43	4.1	8.2	5.5	4.4	5.0	5.4	5.5	6.1	3.1	5.0	5.4
44	3.2	6.0	4.7	3.8	4.6	5.1	4.2	4.6	1.6	3.8	4.3
45	0.8	7.0	4.3	3.7	3.5	4.8	3.2	4.5	1.2	3.1	3.6
46	1.6	5.0	3.3	3.7	3.0	2.1	2.0	3.1	0.9	2.8	2.7
47	1.6	2.7	1.6	2.5	1.8	2.9	2.2	1.6	0.6	2.3	2.0
48	1.6	2.4	1.3	2.2	0.8	1.5	1.3	1.0	0.6	1.2	1.3
49	0.8	0.7	0.9	1.7	0.7	1.1	0.7	0.6	0.1	0.7	0.7
50	0.8	0.6	0.6	0.5	0.4	0.6	0.5	0.4	0.1	0.3	0.5
51	0.0	0.0	0.3	0.5	0.1	0.1	0.2	0.2	0.2	0.1	0.1
52	0.0	0.0	0.1	0.2	0.0	0.1	0.1	0.0	0.2	0.1	0.1
53	0.0	0.0	0.0	0.1	0.0	0.0	0.1	0.1	0.0	0.0	0.0
No. sampled	250	1229	3174	902	3214	2064	3219	2991	1436		

^a In computing the 1944-53 mean, the 1947 data have been excluded (see text).



On the Distribution of Young Sockeye Salmon (*Oncorhynchus nerka*) in Babine and Nilkitkwa Lakes, B.C.¹

By W. E. JOHNSON
Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

ABSTRACT

Babine Lake and connected Nilkitkwa Lake, a total lake area of 174 square miles, provide nursery facilities for progeny of the largest sockeye salmon run to the Skeena River in northern British Columbia.

Based on catch per unit of fishing effort, tow-net collections in August and October, 1955, indicate that at least 67%, and possibly as much as 88%, of the total age 0 sockeye population of these lakes (estimated as 50 to 60 million) was concentrated in Nilkitkwa Lake and the North Arm of Babine Lake: that is, in 11.4% of the total lake area. Mean size of young sockeye in these areas of concentration was much smaller than in the sparsely populated remainder of Babine Lake.

This unequal distribution of young sockeye, and resulting inefficient utilization of the lake nursery facilities, is apparently a result of the distribution of the spawning parent population and a limited dispersal of young sockeye from their points of entrance into the lake as fry.

INTRODUCTION

The Babine area (see map, Fig. 2) is the most important sockeye salmon producing area of the Skeena River system in northern British Columbia. Each year since 1946 the Fisheries Research Board of Canada has enumerated the Babine run of adult sockeye by means of a counting fence on the Babine River. Sockeye of the Babine run spawn from late July to late October; the eggs hatch in the spring and the fry begin their period of lake residence during May and June. It is believed that the great majority of any brood spend one year in lake residence and emigrate seaward as one-year-old smolts during the following May and June: the proportion of one-year-olds in samples from the smolt runs of 1950-55 ranged from 98.2% to 100%, the remainder being two-year-olds.

In the Babine area, three nursery areas for young sockeye are accessible: Babine Lake, Nilkitkwa Lake and Morrison Lake. The progeny of sockeye spawning in Tahlo Creek, tributary to Morrison Lake, are believed to spend their freshwater life in Morrison Lake; in addition, some of the progeny of spawning in upper reaches of the Morrison River may utilize that nursery area. However, the number of sockeye spawning in these areas is a very small percentage of any run (e.g., less than 5% of the 1954 run). All except this small percentage spawn in areas immediately tributary to Babine and Nilkitkwa lakes, and their progeny are believed to spend their freshwater phase of life in these two lakes.

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The general belief has been that the sockeye fry produced in areas tributary to Babine and Nilkitkwa lakes become generally dispersed throughout these lakes and utilize the nursery facilities available as a whole during their lake phase of life.

During the course of two visits to the Babine area in August and October, 1955, a total of 979 young sockeye salmon were captured in Nilkitkwa and Babine Lakes. Only 11 were more than one year old; the remaining 968 were of age 0: that is, they were progeny of adults spawning in 1954 and had entered the lakes as fry in the spring of 1955. This paper presents an analysis of the distribution of age 0 sockeye salmon in Babine and Nilkitkwa lakes based on these collections. In addition, the indicated distribution of young sockeye is discussed, particularly with respect to the distribution of the spawning parent population and lake morphometry.

METHOD OF CAPTURING YOUNG SOCKEYE

Basic investigations of lakes which produce sockeye salmon have been greatly hampered in the past by the lack of a satisfactory method for obtaining representative samples of the young pelagic sockeye during their period of lake residence. The method by which these samples were obtained was developed and first used by the author at Lakelse Lake, B.C., in 1954; since then, it has been successfully employed on other lakes of the Skeena River system and on Shuswap Lake in the Fraser River system.

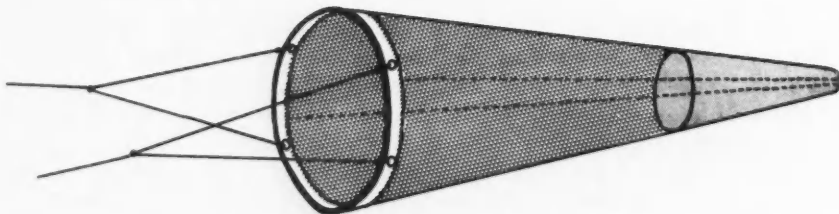


FIG. 1.—Diagram of the tow-net, showing the attachment of tow lines from the two boats.

This method of capture involves the use of a tow-net towed by means of two boats powered with outboard motors. A diagram of the tow-net is presented in Figure 1. This net is simply a cone-shaped bag, the open mouth end of which is given rigidity by means of a ring of $\frac{5}{16}$ -inch stainless steel rod. The size found most suitable for the towing power ordinarily available (15- to 25-horsepower outboard motors) has been a net nine feet in length with a mouth diameter of three feet. The use of $\frac{5}{8}$ -inch (stretched measure) nylon netting for the forward six feet of the net and woven nylon material with openings of approximately $\frac{5}{32}$ inch for the three-foot bag end has proved satisfactory for the capture of young sockeye, including the small, newly-emerged fry.

The net is towed by two boats running parallel about 100 feet apart; in this manner, nothing directly precedes the mouth of the net while towing. For

surface tows (which fish the surface three feet with the net of three-foot mouth diameter) each boat is equipped with a 100-foot tow line of $\frac{1}{4}$ -inch nylon rope. In order to fish at greater depths, it is necessary to attach weights or depressors to the tow lines; depth of fishing is approximately from the angle and length of the tow lines, and is regulated by varying the length of the tow lines. Such tows at greater depths require greater towing power, longer tow lines of wire rope and winches for hauling the net.

Experience has shown an overwhelmingly greater fishing success of surface tows. However, of primary importance in the capture of young sockeye with such surface tows is the time of day at which fishing is carried out. Tows made during daylight hours are very rarely successful, even when schools of young sockeye are observed active at the surface. In the evening twilight, as dusk approaches, fishing success increases quickly and reaches a maximum during the first moments of darkness. Then, fishing success decreases and catches are rare during the remaining hours of darkness. No such period of high catchability has been observed for the morning twilight period. This same daily pattern of catchability has been observed in all sockeye lakes where this net has been used, including Nilkitkwa Lake and the different regions of Babine Lake where towing was carried out.

Based on this experience, the following routine method of sampling was adopted: Surface tows of 10 to 15 minutes duration, towing at a speed of approximately 7 miles per hour, are made consecutively for one hour in the evening, spanning the period of dusk and early darkness. This hour of towing is used as the unit of fishing effort. Towing is carried out at random in the pelagial (offshore) zone of the lake.

Since adopting this standard method of sampling in August, 1955, experience at Lakelse Lake points to the consistency of this manner of sampling young sockeye populations. The mean size and variance in size of sockeye shown by repeated samples taken on successive days was quite constant. The catch per hour of towing in the evening, spanning the period of high catchability, showed relatively small variation in repeated samplings; however, catchability did change seasonally, being much lower in the fall than during the summer period. This might suggest that catchability decreases with an increase in size of the young sockeye; however, it will be noted later that the proportional decrease in catch per effort from summer to fall is evident over a great range in mean size of sockeye. The greatly lowered catchability in the fall as compared with summer is believed to be a result of behaviour changes associated with lower temperatures and other environmental changes accompanying the fall overturn in lakes. Relatively small variation in catch per unit of effort of repeated samplings by towing randomly in the offshore zone indicated a generally uniform offshore distribution of young sockeye at Lakelse Lake (area, 5.2 square miles). Also at Lakelse Lake, during periods of complete calm great numbers of active schools of young sockeye at the surface have been observed frequently; this surface activity, although restricted to offshore regions (depths greater than 2 metres), suggests a generally uniform distribution over the entire offshore area of this small, single-basin lake.

The samples from Babine and Nilkitkwa lakes with which we are concerned were all taken by means of surface tows, towing at a speed of approximately 7 miles per hour. On each sampling date 10- to 15-minute surface tows were made consecutively for one hour in the evening spanning the period of dusk and early darkness; one such hour of towing is used as the unit of fishing effort. All towing was carried out in the pelagial zones of the indicated locations.

It is assumed that the samples of sockeye obtained are random and reasonably representative of the populations present. It is also assumed that, during the time interval of these series of collections, the catch per unit of effort was related approximately proportionately to population density in the general area where towing was carried out.

RESULTS

BASIC DATA

The first series of collections of young sockeye was made during the period 21-27 August 1955. Surface towing, as described above, was carried out in 4 locations, in Nilkitkwa Lake and in 3 areas of Babine Lake: (1) the North Arm of Babine Lake, between the outlet (Ft. Babine) and 5 Mile Creek; (2) central Babine Lake, between the Fulton River and Sockeye Creek; and (3) southern Babine Lake, between Pendleton Creek and 15 Mile Creek. (See map, Fig. 2.) The results of this series are given in Table I.

TABLE I.—Age 0 sockeye taken in surface tows: 21-27 August 1955. Each date indicates one hour of surface towing in the evening of that day, spanning the period of dusk and early darkness.

Location	Date, Aug. 1955	Number of sockeye		Size of sockeye			
		Total catch	Catch per hour	Mean weight	Range in weight	Standard devia- tion	95% confidence limits
<i>grams grams grams grams</i>							
North of Halifax Narrows:							
Nilkitkwa Lake	21	384	384	0.84	0.3-2.7	0.38	0.80-0.88
North Arm of Babine Lake*	22	342	342	1.22	0.3-2.8	0.48	1.17-1.27
South of Halifax Narrows:							
Central Babine Lake ^b	24 and 27	18	9	2.09	0.5-4.0	1.07	1.56-2.62
Southern Babine Lake ^c	25 and 26	6	3	2.05	1.0-3.3	0.82	1.19-2.91

*In the area between the outlet (Ft. Babine) and 5 Mile Creek.

^bIn the area between the Fulton River and Sockeye Creek.

^cIn the area between Donald's Creek and 15 Mile Creek.

The second series of collections was carried out during the period 11-18 October 1955. In this series, surface towing was carried out in the same 4 locations as the August series, plus 2 additional locations: the Morrison Arm of Babine Lake, and that part of the North Arm of Babine Lake immediately north of Halifax Narrows (Fig. 2). The results of this series of tows are given in Table II. Catch per hour was considerably lower in the October series than in August. The fact that it was proportionately lower in all cases, regardless of size

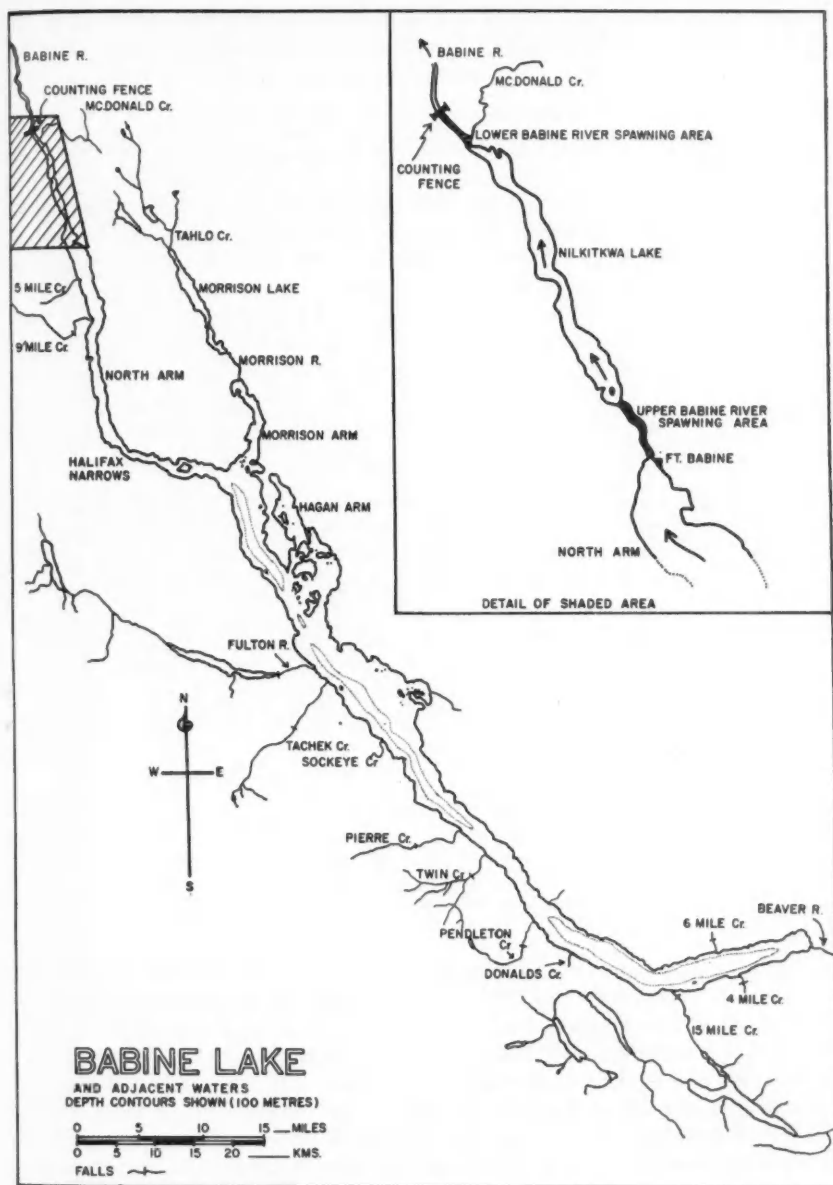


FIG. 2.—Map of Babine Lake and adjacent waters.

of the sockeye, supports the view expressed above that the lowered catchability in the fall is associated with lower temperature and general environmental changes which accompany the fall overturn in lakes.

EVIDENCE OF UNEQUAL DISTRIBUTION OF YOUNG SOCKEYE

Catch per unit of fishing effort is commonly used as an indication of population density, and it is assumed that catch per unit of effort within each area during the time interval of each of these series of collections was approximately proportional to the density of the sockeye population present. Differences in mean size of individuals have also been used as an indication of differences in population density; this point is discussed below.

Based on differences in catch per unit of effort and in mean size of individuals, within the time interval of each series, the data of Tables I and II offer evidence of a highly unequal distribution of the young sockeye utilizing the Babine-Nilkitkwa nursery area. The much higher catch per unit of effort and smaller size of sockeye indicate populations of much higher density in all areas north of Halifax Narrows as compared to all areas south of that point.

TABLE II.—Age 0 sockeye taken in surface tows: 11-18 October 1955. Each date indicates one hour of surface towing in the evening of that day, spanning the period of dusk and early darkness.

Location	Date, Oct. 1955	Number of sockeye		Size of sockeye			
		Total catch	Catch per hour	Mean	Range	Standard	95%
				weight	in weight	devia- tion	confidence
				grams	grams	grams	limits
North of Halifax Narrows:							
Nilkitkwa Lake	17	97	97	1.13	0.4-2.8	0.52	1.03-1.23
North Arm of Babine Lake ^a	16	57	57	1.36	0.5-3.3	0.65	1.19-1.53
North Arm of Babine Lake ^b	18	59	59	1.68	0.6-3.5	0.59	1.53-1.83
South of Halifax Narrows:							
Morrison Arm	15	0	0
Central Babine Lake ^c	14	4	4	3.3	1.9-3.9
Southern Babine Lake ^d	11 and 12	1	0.5	3.9

^aIn the area between the outlet (Ft. Babine) and 5 Mile Creek.

^bIn the area immediately north of Halifax Narrows.

^cIn the area between the Fulton River and Sockeye Creek.

^dIn the area between Donald's Creek and 15 Mile Creek.

AREAS NORTH OF HALIFAX NARROWS: The highest catch per unit of effort and the smallest mean size of sockeye, for both series of collections, indicate the greatest density of young sockeye in Nilkitkwa Lake.

Within the North Arm of Babine Lake, all collections indicate a population of high density. Comparing the two locations sampled in October, the almost equal catches per hour fail to suggest differences in density within the Arm, but these are based on only one hour of towing in each area. Evidence of some diversity is provided by the greater mean size of the sockeye in the area immediately north of Halifax Narrows, which in turn may reflect a smaller population density than in the more northern part of the Arm.

AREAS SOUTH OF HALIFAX NARROWS: The extremely low catch per unit of effort in all areas sampled south of Halifax Narrows indicates a general low density of young sockeye throughout this major portion of Babine Lake. In the August sample from central Babine Lake the mean size of sockeye is significantly greater than in any samples from north of Halifax Narrows; and the three smaller samples from south of Halifax Narrows all include individuals larger than any taken north of that point at the corresponding season. Mean size of the sockeye south of the Narrows is comparable to that of sockeye in sparsely-populated Lakelse Lake; there is certainly no evidence of slow growth owing to competition.

Within the region south of Halifax Narrows, greater catches per unit of effort give some indication of a higher density of sockeye in the central Babine Lake area than in the southern area and Morrison Arm.

CAUSE OF DIFFERENCES IN GROWTH RATE: Differences in rate of growth of different stocks might be a result of different physical environments, differences in food supply which are independent of size of stock, or differences in stock density (which would probably act by way of a greater drain on food supply by larger populations). 1. At Babine the main body of the lake, south of Halifax Narrows, has much the same summer temperature as the North Arm. Nilkitkwa Lake is warmer and is little stratified thermally, conditions which would probably increase, not decrease, rate of growth: the temperatures achieved do not exceed the optimum for sockeye (Brett, 1952). 2. Basic productive potential for crustacean plankton in the North Arm should be similar to that in the main lake, since it contains water of similar mineral content and similar temperature. Nilkitkwa Lake is probably potentially more productive, because warmer and shallower, which would make for more rapid growth of stock of any given density per unit area.

Evidently the physical characteristics, as far as known, would favour an increased rate of growth, moving from south to north and from Babine Lake to Nilkitkwa Lake. The observed trend is the reverse of this, and it seems reasonable to ascribe it to the effects of population density—greater density making for slow growth. Foerster (1944) demonstrated a similar inverse relation between density of stock and size of young sockeye, by comparing years having populations of different sizes.

Results (unpublished) of extensive plankton sampling throughout Babine and Nilkitkwa Lakes during the August period may also reflect differences in density of sockeye populations. In all areas sampled north of Halifax Narrows, crustacean plankters were extremely scarce in comparison with all areas sampled south of that point. Since the basic productive potential in the southern area is no less than in the northern, this difference is presumably a result of intensive foraging by the dense populations north of the Narrows. Similarly, at Cultus Lake Ricker (1937) found that in a year of large sockeye population the abundance of zooplankton food in August was low as compared with several years of much smaller populations.

DISTRIBUTION OF AGE 0 SOCKEYE IN THE BABINE-NILKITKWA NURSERY AREA

If catch per unit of fishing effort is related proportionately to population density, the product of catch per unit of effort and area is an index of population size. Assuming that catch per unit of effort was approximately proportionately related to density within each area during the time interval of each series, the products of catch per hour and area, as indices of population size, are computed below for each series of collections. Total lake areas are used because schools of sockeye were constantly observed in all but the immediate inshore regions: that is, regions of less than approximately 2 meters depth. This inshore region is a very small percentage of the area of any of the lakes with which this paper deals.

Locality	Area	August		October	
		Mean catch	Area \times mean catch	Mean catch	Area \times mean catch
	<i>acres</i>	<i>fish/hour</i>		<i>fish/hour</i>	
Nilkitkwa Lake	1,200	384	461,000	97	116,000
North Arm of Babine Lake	11,500	342	3,933,000	58	667,000
Babine Lake south of Halifax Narrows	98,500	6	591,000	1.5	148,000
Totals	111,200		4,985,000		931,000

These indices of population size indicate the following distribution of the age 0 sockeye population in Babine-Nilkitkwa nursery area, in terms of percentage of the total:

Locality	Area	August sockeye population	October sockeye population
	%	%	%
Nilkitkwa Lake	1.1	9.2	12.5
North Arm of Babine Lake	10.3	78.9	71.6
Babine Lake south of Halifax Narrows	88.6	11.9	15.9

These estimates of distribution, based on each of the two series independently, are in good agreement.

Regarding the low percentage (11.9% and 15.9%) indicated as being in the large area south of Halifax Narrows: the computations were made assuming that the mean of the catches per hour in the areas sampled (2 areas sampled in August and 3 in October) was representative of this entire large area; it may be that the highest catches in central Babine (9 per hour in August and 4 per hour in October) are representative of density in a larger portion of this region that such procedure assumes. However, even if these highest catches were used as a measure of density everywhere south of Halifax Narrows, the computations indicated that only 17% (August) and 33% (October) of the sockeye are in this region.

INDICATIONS OF ABSOLUTE POPULATION SIZE

It is interesting to speculate as to the actual size of the populations with which we are dealing. This can be done by comparing catch per effort data with that from Lakelse Lake, where surface towing was carried out in exactly the same manner at approximately the same times of the year and where knowledge of the approximate size of the age 0 sockeye population is available.

At Lakelse Lake an estimated 2,800,000 fry entered the lake in the spring of 1955, the peak of this fry run occurring in mid-May (McDonald and Shepard, 1955, and personal communication). Assuming a mortality trend during lake residence similar to that found at Cultus Lake (Foerster, 1938), and taking into account an indicated higher total survival from fry to smolt in Lakelse Lake, it is likely that approximately 40% of the fry input survived at the end of August and 35% at the end of October. That is, there were an estimated 1,120,000 age 0 sockeye (336 per acre) present in Lakelse Lake at the end of August, 1955, and 980,000 (294 per acre) at the end of October, 1955. Ten units of fishing effort (each unit indicating one hour of surface towing in the evening spanning the period of dusk and early darkness) at Lakelse Lake during late August and early September captured 280 age 0 sockeye, or 28 per unit of effort. Two units of effort in late October captured 12 sockeye, or 6 per unit of effort. Taking these catches as standards relating catch per effort to population density during these periods of time, and assuming that catch per effort is related proportionately to population density at all levels and in the different lakes concerned, the following estimates of population density are obtained:

Locality	August 1955		October 1955	
	Catch	Sockeye population	Catch	Sockeye population
	<i>fish/hour</i>	<i>fish/acre</i>	<i>fish/hour</i>	<i>fish/acre</i>
Lakelse Lake	28	336	6	294
Nilkitkwa Lake	384	4,608	97	4,753
North Arm of Babine Lake	342	4,104	58	2,842
Babine Lake south of Halifax Narrows	6	72	1.5	74

From these figures the number of sockeye in Babine Lake and Nilkitkwa Lake can be estimated as follows:

Locality	Area in acres	Number of age 0 sockeye salmon	
		August 1955	October 1955
Nilkitkwa Lake	1,200	5,530,000	5,704,000
North Arm of Babine Lake	11,500	47,196,000	32,683,000
Babine Lake south of Halifax Narrows	98,500	7,092,000	7,289,000
Totals	111,200	59,818,000	45,676,000

Again considering the area south of Halifax Narrows, computations based on the highest catch per unit of effort in that area have been made, which give an estimated density of 108 sockeye per acre in August and 196 per acre in October. This corresponds to a population of 10,638,000 in August and of 19,306,000 in October for the area of Babine Lake south of Halifax Narrows; and a total population of 63,364,000 in August and 57,693,000 in October.

A further indication of density of the young sockeye populations in Nilkitkwa Lake and the North Arm of Babine can be obtained by referring to the relation of size of young sockeye salmon to lake population density as shown by Foerster (1944) at Cultus Lake, B.C. For the period 1927 to 1935 at Cultus Lake, Foerster demonstrated a high inverse correlation between average weight of emigrating smolts and population size as indicated by the number of emigrating smolts. In 1929 and 1933, with approximately 2.5 and 1.5 million yearling smolts emigrating, the mean size of smolts was quite small (3.06 grams and 3.67 grams). The extremely small size of young sockeye in Nilkitkwa Lake and the North Arm of Babine Lake suggests at least as high a density of population. Based on Foerster's (1938) demonstration of the mortality trend among young sockeye during lake residence, 2 million yearling sockeye smolts emigrating from Cultus Lake in the spring would indicate a total population in the lake of approximately 6 million during the previous September. This would be a lake population density of 3871 sockeye per acre (area of Cultus Lake is 1550 acres) which is comparable to densities indicated above for Nilkitkwa Lake and the North Arm of Babine Lake (4608, 4753, 4104 and 2842 sockeye per acre).

Although this paper is based on a relatively small number of samples for such a large lake area, the obvious indications of the data at hand are felt to justify the general conclusions made regarding unequal distribution, even if the computations of percentage distribution and population size be only grossly indicative of the actual.

FACTORS RESPONSIBLE FOR UNEQUAL DISTRIBUTION OF YOUNG SOCKEYE

The point of entrance of young sockeye as fry into a lake nursery area is of course dependent on the location of the tributary spawning grounds; that is, initial distribution is determined by the distribution of the spawning parent population. The general belief that young sockeye effectively utilize the facilities of the nursery area they enter assumes complete dispersal throughout the nursery area from the point, or points, where they enter as fry.

DISTRIBUTION OF THE SPAWNING PARENT POPULATION

The parent population to the age 0 sockeye with which this paper deals was the 1954 adult run; 503,422 adult sockeye were enumerated as they migrated up the Babine River through the counting fence. Information on the distribution of these sockeye on the spawning grounds is available through the Department of Fisheries, whose officer and assistants made estimates of the number of sockeye on the spawning grounds by frequent visits throughout the spawning season. Based on these estimates, Table III shows the distribution of spawning sockeye of the 1954 run to the Babine area. The close correspondence of the total of estimates made on the spawning grounds (453,300) with the number of sockeye

counted through the counting fence (503,422) lends confidence in the reliability of these estimates.

Referring to Table III and Figure 2, an estimated 241,700 sockeye (56% of the estimated total spawning tributary to Babine and Nilkitkwa Lakes) spawned in areas connected with Nilkitkwa Lake and the North Arm of Babine Lake; nearly all of these fish spawned in the outlet spawning areas of the upper and lower Babine River. Only 44% spawned in areas tributary to the 88.6% of the nursery area south of Halifax Narrows. Based on the more stable conditions of water flow, it is a generally accepted view that percentage survival from egg to fry is probably greater in lake outlet spawning areas than in runoff stream spawning areas; considering this, it is probable that even more than 56% of the fry produced by the 1954 spawning originated from spawning areas north of Halifax Narrows.

TABLE III.—Distribution of spawning sockeye salmon in Babine Lake area, 1954. Based on Department of Fisheries forms B. C. 16, Salmon stream spawning reports, 1954.

Spawning area	Estimated number of spawning sockeye
TRIBUTARY TO NILKITKWA LAKE AND THE NORTH ARM OF BABINE LAKE:	
Upper Babine River	140,000
Lower Babine River	100,000
McDonald Creek	400
5 Mile Creek	300
9 Mile Creek	1,000
Subtotal	241,700
TRIBUTARY TO BABINE LAKE SOUTH OF HALIFAX NARROWS:	
Morrison River ^a	12,000
Fulton River	110,000
Tachek Creek	1,900
Sockeye Creek	900
Pierre Creek	17,000
Twin Creek	14,000
Pendleton Creek	1,100
Kew Creek	300
Donald's Creek	300
15 Mile Creek	25,000
6 Mile Creek	1,800
4 Mile Creek	2,200
Grizzly Creek (branch of Beaver River)	3,100
Subtotal	189,600
Total ^b	431,300

^aSome of the progeny of sockeye spawning in the Morrison River may move upstream into Morrison Lake.

^bIn addition, an estimated 12,000 sockeye spawned in Tahlo Creek; however, because progeny of these fish are believed to spend their freshwater life in Morrison Lake, they are of no concern to this paper.

The indicated concentration of young sockeye north of Halifax Narrows corresponds with this concentration of the parent population in spawning areas north of that point. Further relationships are noted: Nilkitkwa Lake, in a position to receive the greatest concentration of fry, has the greatest density of young sockeye. In the North Arm of Babine Lake, most of the fry enter from the outlet at the north end and the northern part of the North Arm has a greater density of young sockeye than the southern part (immediately north of Halifax Narrows). In the part of Babine Lake south of Halifax Narrows, number of spawners indicates that more than half of the fry enter that region from the Fulton River; the adjacent central Babine area showed the greatest density of young sockeye in areas sampled south of Halifax Narrows.

These relationships between distribution of the spawning parent population and the observed distribution of young sockeye in the lake give evidence of a limited dispersal of young sockeye from the point where they enter the lake nursery areas as fry.

LIMITED DISPERSAL OF YOUNG SOCKEYE FROM THEIR POINT OF ENTRANCE AS FRY

With this evidence of a limited dispersal of young sockeye from their point of entrance as fry, it is of interest to speculate on the mechanisms of such dispersal.

Great numbers of newly emerged sockeye fry have been observed as a massed living band moving upstream from the lower Babine River spawning area into Nilkitkwa Lake and from the upper Babine River spawning area into the North Arm of Babine Lake (F. C. Withler and K. V. Aro, personal communication). (No information on the extent or existence of any movement of fry from the lower Babine River spawning area through Nilkitkwa Lake into Babine Lake is available.) This same phenomenon has been observed at Shuswap Lake in the Fraser system, B.C. and at that lake a mass movement has been noted to extend along the lakeshore for several miles uplake from the outlet (D. R. Foskett, personal communication). I am unaware of any observation of such migration of sockeye fry in lakes over the distance involved between the outlet of Babine Lake and Halifax Narrows (19 miles).

The movement of fry upstream is presumably a result of their positive response to current (Hoar, 1954). Once the fry have entered the lake, current presumably would remain the stimulus leading to further directed movement, or perhaps they might follow the shorelines. The dependence of lake currents on wind direction, and the existence of more or less independent regions of circulation in multibasin lakes and along the length of extremely long, narrow basins would indicate that currents offer no direct guide to remote regions of lakes such as Babine. If the fry follow the shorelines, it would also be a long and circuitous route to remote areas of the lake. In either case, or even if they could follow the most direct route, it seems unlikely that newly emerged fry are sufficiently equipped with energy reserves to undertake a migration of any great distance.

Tow-net sampling at Lakelse Lake during the fry run of 1955 indicated that the newly emerged fry took up a pelagic, plankton-feeding existence very soon

after entering the lake. It would seem reasonable to suppose that sockeye fry in general must commence feeding within a relatively short time. Once they start feeding the drive to obtain food probably dominates their freshwater life until the drive leading to seaward emigration develops.

Assuming then that sockeye fry must and do begin feeding reasonably soon after emergence and that they do take up a pelagic, plankton-feeding existence, this occurs relatively close to the point where they entered the lake as fry. Once having taken up a pelagic existence, whether they feed at random on plankton or seek out concentrations, they are subject to being carried along with their plankton food in the general circulation of the water mass. For this reason, it seems unlikely that they would chance to leave the circulating water mass of which they are a part, whether that water mass be one lake or an independently circulating water mass within one lake. Regarding multibasin lakes or extremely long, narrow basins, the movement of young sockeye from one region of circulation (water mass) to another is probably one of chance, dependent on the extent of intercirculation between adjacent regions of circulation.

Temperature profiles taken in different regions of Babine Lake during both August and October, 1955, indicate regions of quite independent circulation, even within the North Arm (Johnson, MS). If movement of young sockeye is dependent on the extent of intercirculation between adjacent water masses, Halifax Narrows poses the greatest natural barrier to dispersal of young sockeye in Babine Lake: it is only a quarter of a mile wide and its average depth is about 10 metres. The high percentage of young sockeye which remain north of Halifax Narrows points to the barrier effect of this narrows. Although adjacent regions of circulation are less distinctly separated in the remainder of Babine Lake, all the data point to a limited dispersal of young sockeye from their point of entrance into the lake. Although a gradual dispersal probably goes on during the whole phase of lake residence, the October collections (nearly 6 months after their entrance as fry) suggest incomplete dispersal of young sockeye even within the North Arm. The distribution of young sockeye salmon in the Babine-Nilkitkwa lakes nursery area indicated in this paper is in full agreement with this concept of a limited dispersal from their point of entry as fry.

CONCLUDING REMARKS

The evidence presented in this paper suggests that the distribution of young sockeye salmon may in general be dependent on the distribution of their spawning parent population and the morphometry of the lake. If so, these findings are of significance to the management of this important fishery. There are a number of large, sockeye salmon producing lakes of the multibasin type, or with long and narrow basins, within which one would expect to find regions of independent circulation; where this is combined with unequal distribution of the tributary spawning grounds, or with concentration of spawning populations on only some of the spawning grounds available, an unequal distribution of young sockeye is indicated. In order to fully utilize such lake nursery areas and attain maximum production, distribution of spawners to all available spawning areas or dispersal of young sockeye by whatever other means feasible is essential. Also, with

survival to adult size dependent on smolt size (Foerster, 1954), widespread distribution of spawners to all available spawning grounds should provide best use of escapements even below the maximum. Unequal distribution of spawning grounds may account for the previously unexplainable low production of some large lakes of this type. Similarly, even where there is a wide distribution of spawning grounds, a concentration of escapements on only some of these may account for the failure of present management to attain previously known higher levels of production.

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During the period July, 1954, to July, 1955, when the method of capture essential to this study was developed, the author was a postdoctoral fellow of the United States National Science Foundation. Dr. M. P. Shepard, in charge of the Lakelse Lake field station of the Fisheries Research Board of Canada, assisted in innumerable ways during that period.

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The Oceanography of Hebron Fjord, Labrador^{1,2}

BY DAVID C. NUTT³ AND LAWRENCE K. COACHMAN⁴
Dartmouth College, Hanover, N.H., U.S.A.

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ABSTRACT

Hebron Fjord, extending some 28 miles into the northeast coast of Labrador at about latitude $58^{\circ}10'$ N., and having a sill at depth of 59 m. across its mouth, was visited at various periods during 1949, 1952 and 1954. The present paper deals with the oceanographic regime and physical environment in the fjord and adjacent coastal waters. Data on tides and currents, and on contributions of fresh water from precipitation run-off and ice melting are given. Oceanographic factors discussed include temperature, salinity, dissolved oxygen, inorganic phosphate, temperature-salinity relationships, and long-term trends. Ice formation as an oceanographic phenomenon is considered. Computations of thermohaline convection are made, and the effects of ice formation and exchange in determining the winter oceanographic structure are discussed. Above sill depth exchange occurs principally by horizontal movements and a flushing

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³Research Associate in Geography, Dartmouth College, Hanover, N.H.

⁴Research Assistant in Northern Studies, Dartmouth College, Hanover, N.H.

time of about 68 days is computed. Below sill depth exchange must involve vertical movements and occurs principally by convection in winter. Calculations of the A factors of eddy conductivity and eddy diffusivity are made. Dynamic computations of water transport are given. During winter a water temperature of $-1.75^{\circ}\text{C}.$ exists at all levels in the fjord, rising in summer only to -1.68° at 250 m. and -1.00° at 100 m., causing the bottom waters to remain an isolated pocket of high Arctic environment during the summer and fall seasons as contrasted with the disappearance of negative temperatures down to 120 m. by mid-October outside the fjord. Inorganic phosphate increases with depth; photosynthesis maintains oxygen at super-saturation above 30 m. during summer, and the rate of oxygen consumption and renewal by vertical transport below 80 m. is calculated.

I. INTRODUCTION

LABRADOR forms the easternmost extension of the North American continent. Its coast is much indented by bays and fjords of varying topographic arrangement. The cold Labrador Current flows south from Hudson and Davis Straits along the continental shelf and slope carrying with it extremely cold Arctic water to the relatively low latitudes off Labrador and Newfoundland and preventing true Atlantic water from reaching the coasts (Nutt, 1953). While earlier work has described or defined the Labrador Current (Iselin, 1932; Smith, Soule and Mosby, 1937; Bailey and Hachey, 1951b), our knowledge of the immediate coastal waters is restricted to the single observation of temperature in Nachvak Fjord made by the Brown Harvard Expedition of 1900 (Delabarre, 1902); the few hydrographic stations in Nachvak, Saglek, and Ekortarsuk Fjords by the *Chance* in 1926 (Iselin, 1932); and the early studies of the *Blue Dolphin* (Nutt, 1953).

As a part of the extensive investigations of the Labrador coastal waters carried out by the research vessel *Blue Dolphin*, a specific study of the oceanography of Hebron Fjord, situated on the northeast coast of Labrador at latitude $58^{\circ}10' \text{ N}.$, was completed in the fall of 1954. This detailed study had been prompted by the finding of an extremely low-temperature ($-1.8^{\circ}\text{C}.$) marine environment at the lower levels of Hebron Fjord in 1949 which was believed to persist throughout the year. The adaptation and physiology of the marine bottom fauna in relation to this environment raised some interesting problems which were the subject of a detailed investigation of this fjord during 1954 and 1955. The physiological research has been conducted by Dr. Per F. Scholander⁵ and his co-workers at the Woods Hole Oceanographic Institution and will be reported elsewhere. This paper deals with the oceanographic regime and physical environment in Hebron Fjord and in the adjacent coastal waters.

During the course of the *Blue Dolphin* Labrador Expeditions from 1949 to 1954 Hebron Fjord was examined at the following times: 1949, August 7-12; 1952, July 19, 23, 31; 1954, March 26 to April 6, July 9 to August 12, and October 15-26. On the occasion of each visit observations were taken for the determination of surface and subsurface temperatures, salinities and, at certain stations, for dissolved oxygen and inorganic phosphates. The station locations within Hebron Fjord and in the immediate coastal waters are given in Figure 1.

⁵Now at the Institute of Zoophysiology, University of Oslo, Norway.

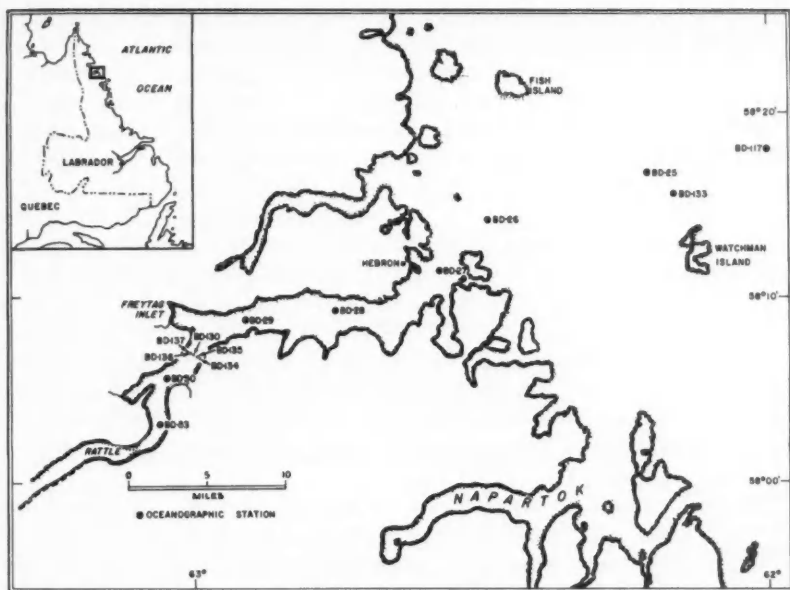


Figure 1. HEBRON FJORD, LABRADOR.

Temperature observations were taken by means of both bathythermograph (BT) and protected deep-sea reversing thermometers. All instruments were calibrated at the Woods Hole Oceanographic Institution. As the depths involved were not great, the depth of observation was determined by the length of submerged wire \times the cosine of the wire angle with the vertical.

Water samples were taken by means of Nansen bottles. Determinations for dissolved oxygen and inorganic phosphate were made in every case on board the vessel. The Winkler method was used for oxygen, while the phosphate determinations were made colorimetrically. In 1952 these were done by comparison with standards and the results are considered of only limited accuracy. In 1954 an electric eye photometer (EEP) was used.

The chlorinity titrations were made by the Knudsen method. In some cases these were done at the Woods Hole Oceanographic Institution and in some cases on board the *Blue Dolphin*. In cases where titrations were performed on board, certain selected samples were kept and returned for check titration at Woods Hole. In most cases substantial agreement was found between the shipboard results and the results at Woods Hole, so it is felt that shipboard titrations had a maximum probable error of $\pm 0.05\%$.

Observations during the summer months were made in a routine manner from the *Blue Dolphin*. The fall observations in 1954 were made from a motorboat with hand winch and temporary A-frame. Winter regime observations during March 1954 were made through the ice from a pyramidal tent, with the

hand winch and metre wheel mounted on the specially designed tent frame (Nutt, 1952). It might be added that winter water samples were taken in the usual 6-ounce rubber-stoppered glass bottles which were filled only three-quarters full and allowed to freeze. No damage to the bottles was incurred and the validity of the samples is clearly indicated by the results, which show an almost completely isohaline structure within extremely narrow limits of $\pm 0.01\%$.

1. BATHYMETRY

Offshore from Hebron Fjord are very few islands and the bottom topography is quite irregular, varying in depth from 75 to 200 m. Between Hebron and Cape Chidley at the northern tip of Labrador there are large areas dotted with islands and shoal ground.

In the mouth of the fjord is Kingmiktok (Island), approximately 2 miles long; and between it and the mainland to the south is a very shallow channel $\frac{1}{2}$ mile wide. The main entrance to the fjord is to the north of the island and is 2 miles wide. A sill with a maximum depth of approximately 59 m. lies across this entrance.

The fjord extends uniformly to the west about 18 miles and then to the southwest another 10 miles. The average width is 1.8 miles. The shores are regular and steep-to, and are indented by four bays on the south shore and three bays on the north.

The fjord bottom topography is shown in the vertical profiles of temperature and salinity (e.g. Fig. 2). Beyond the innermost station, BD-33, is an unexamined area approximately 8 miles long. The connection between this area and the fjord appears to be narrow and shallow.

The fresh water enters the fjord at various locations along either side. The major streams, none of which are large, enter the fjord at four points: in Freytag Inlet, on the south shore 20 miles from the mouth, in an inlet 23 miles from the entrance on the northwest shore, and at the head of the fjord.

2. CLIMATE

The climate of northern Labrador shows considerable variation from season to season and from the coast to the interior. During the winter months Labrador lies between the Icelandic low and the North American continental high which produces a prevailing northwesterly airflow and low winter temperatures. However, easterly winds off the comparatively warm Labrador Sea provide a moderating influence on the temperatures and the possibility of short periods of near- or above-freezing temperatures during any month of winter. During summer the Icelandic low as well as the continental high dissipate, and a weak low appears over Hudson Strait and southern Baffin Island. Then the prevailing airflow is from the west and southwest which, with the continental heat of summer, can bring temperatures in Labrador into the 80's and 90's (Fahrenheit). However, due to intense land warming these westerly winds are often replaced along the immediate coastal fringe by a sea breeze that brings in cold air and fog from the ice pack and cold Labrador Current.

In Labrador the heaviest precipitation occurs in the southern part with an annual total of about 40 inches near Battle Harbour. Amounts of precipitation decrease regularly northward until at Resolution Island in Hudson Strait there is a total of only 16 inches.

Recent climatological observations at Hebron (Department of Transport, 1954) are based on only 4 years of record. Temperature data from this short period are deemed of sufficient accuracy for the purposes of this paper to indicate the general annual temperature regime.

On the other hand this 4-year period is not considered long enough in the case of the precipitation data on which freshwater run-off computations are based, especially as the general pattern of seasonal distribution of precipitation is in disagreement with that of the nearby stations of Nain, Hopedale, Indian House Lake and Resolution Island, where longer periods of observation are available. In order to arrive at a more representative picture for the precipitation in the Hebron area the following method has been used:

(a) Precipitation data from Hopedale (10 years of record) and from Resolution Island (19 years) have been averaged. Hebron is located approximately midway between these two stations.

(b) The figures arrived at from (a) are weighted 2.5:1 with respect to the actual Hebron data and a weighted average is thus obtained.

This computed precipitation is summarized with the temperature in Table I.

TABLE I.—Climatological data, Hebron Fjord area.

Month	Computed precipitation	Temperature
	<i>inches</i>	<i>°F.</i>
Jan.	1.77	0
Feb.	1.54	-3
Mar.	1.61	10
April	1.62	23
May	1.88	32
June	2.42	40
July	2.15	50
Aug.	2.28	50
Sept.	2.85	40
Oct.	1.52	34
Nov.	1.45	26
Dec.	1.97	14
For year	23.06	Average: 26

3. CONTRIBUTIONS OF FRESH WATER

Since the contribution of fresh water to the fjord water is one of the important factors influencing the hydrographic conditions, an attempt through analysis of precipitation data and watershed area is made to arrive at an approximate figure for the annual cycle of this contribution. The actual drainage area of Hebron Fjord has not been delimited, since certain sections of the interior are to date unmapped. However, an approximate watershed has been assumed and its area computed as $2,658 \times 10^6 \text{ m}^2$. The area of Hebron Fjord itself is $224 \times 10^6 \text{ m}^2$.

The following further assumptions are made:

(a) Precipitation is held in the form of snow from November 1 until May 15, and that the accumulated amount is released into the fjord from May 15 until July 15, by which time the larger part of the snow has been melted. This assumption means that fresh water is added in blocks and shut off suddenly on November 1, whereas actually the change in inflow varies progressively and likely fresh water is added in relatively small quantities well through November, December, and even into January.

(b) Run-off during May and June is equal to 80% of the actual precipitation and the run-off from July 1 until November 1 is equal to 60% of the actual precipitation. The Hebron Fjord drainage area is unforested, with rock outcroppings along the coast and permafrost in the interior. Although these percentages are arbitrary they are believed to be within reason for the area concerned.

(c) The melting of ice and snow cover in the fjord from May 15 to July 1 contributes an amount of fresh water equivalent to the melting of approximately one metre of ice of a salinity of 5‰.

This last assumption may or may not be valid, depending on the particular conditions prevailing in any particular year, but is an estimate of the average condition. At times all or part of the ice may melt in situ, or might break up and be carried outside the fjord to melt in the coastal waters, or as in July of 1954 pack ice from offshore might invade the fjord and make a contribution of fresh water.

The inherent inaccuracies in these assumptions together with the limitations of the available data are recognized, but it is believed that the figures for contributions of fresh water (Table II) present a reasonable picture of the volumes of fresh water involved.

TABLE II.—Contributions of fresh water, Hebron Fjord.

	Jan.	Feb.	Mar.	Apr.	May 1-15	May 15-31	June	July 1-15	July 15-31	Aug.	Sep.	Oct.	Nov. 1-15	Nov. 15-30	Dec.
Precipitation, mm.	45	39	41	41	24	24	61	28	27	58	72	39	18	19	50
Precip. accum. for run-off, mm.	0	0	0	0	0	87 ^a	188 ^a	91 ^a	27	58	72	39	18	0	0
Run-off %	80	80	60	60	60	60	60	60
Fresh water to fjord by run- off ^a , m ³ x 10 ⁶	169.4	366.1	132.9	39.4	84.7	105.1	57.0	26.3
Fresh water direct ^b , m ³ x 10 ⁶	5.4	13.7	6.3	6.0	13.0	16.1	8.7	4.0
Melting of ice, m ³ x 10 ⁶	63.5 ^d	126.9 ^d
Total fresh water, m ³ x 10 ⁶	238.3	506.7	139.2	45.4	97.7	121.2	65.7	30.3

^aWatershed less Fjord $2,434 \times 10^6$ m².

^bFjord 224×10^6 m².

^c25% of total winter accumulation of precipitation runs off during May 15-31, 50% in June and 25% in first half of July.

^dOne metre of ice of salinity 5‰ melts between May 15 and July 1.

4. TIDES AND CURRENTS

Along the greater part of the Labrador Coast the tidal range is from 3 to 6 feet. Only in the extreme northern part of the coast in the vicinity of Cape Chidley do the large tidal ranges that are well known in Ungava and Frobisher Bays begin to occur. Tidal observations were made at the village of Hebron from early July through the end of October 1954 and are summarized as follows:

	July (19 days)	Aug. (31 days)	Sept. (30 days)	Oct. (30 days)
HWI (hr.)	6.47	6.50	6.26	6.06
LWI (hr.)	12.63	12.73	12.70	12.35
MTL (ft.)	3.04	3.16	3.29	3.26
Mean (ft.)	4.18	3.92	4.04	3.81

The average flow of the Labrador Current has been estimated at some 10 miles per day (Iselin, 1932). Smith, Soule, and Mosby (1937) have calculated velocities as high as 38 miles per day. But information as to the nature and velocities of currents in the immediate coastal waters and inlets is conspicuously lacking. The movement of a cold water mass along the immediate coast near Hebron was traced during the summer of 1954 and its movement from north to south shown to be roughly 2 miles per day (see below). Within Hebron Fjord strong currents have never been noted. After a northeast storm on July 13 and 14 which drove pack ice some 20 miles into the fjord it took more than a day for the remnants of this ice to break up and move out to near the mouth of the fjord, which would show a net surface outflow of considerably less than 1 knot over this period. It is believed that velocities within the fjord seldom exceed 2 knots.

II. OCEANOGRAPHIC FACTORS

The oceanographic data show that during midwinter, which oceanographically occurs in April, the fjord water and the coastal water are virtually isothermal and isohaline. The coastal water appears to be very slightly colder than the fjord water, and a small progressive freshening from the coast toward the inner fjord is indicated. The average winter temperatures and salinities in 1954 were:

	Inner fjord	Mid fjord	Coastal
Average temperature, °C.	-1.76	-1.75	-1.78
Average salinity, ‰	32.73	32.75	32.76

These uniform midwinter conditions were altered during the course of the annual cycle by the seasonal changes in the Labrador Current, the climatic changes, and the contributions of fresh water from land drainage and melting ice. However, during the winter of 1955 it was expected that the conditions would again become uniform at very near the same point. (See later for discussion of longer-term trends.)

An examination of the various oceanographic factors now follows.

1. TEMPERATURE

Longitudinal profiles of Hebron Fjord showing the distribution of the temperature ($^{\circ}\text{C}.$) for the times of observation during July, August and October 1954 are given in Figures 2, 3, and 4. As has been noted, the water in winter is isothermal and isohaline, and vertical convection processes are in progress.

The first heat of spring is used in the melting of ice, and heat is transferred to the fjord waters only when the ice surface becomes rotten and broken. However, by the time of the early summer observations on July 9 and 10 warming has taken place in the upper layers and is noticeable down to between 60 and 80 m. It is noted that the $-1.5^{\circ}\text{C}.$ isotherm slopes progressively down from the inner part of the fjord and disappears outside the fjord where heat has penetrated to the very bottom. At station BD-26 even with pack ice of concentration of 0.8 to 0.9 extending 100 miles offshore the temperature at 100 m. is as high as $-1.29^{\circ}\text{C}.$ At this depth the temperature within the fjord remains unchanged from that of winter. There then must be a greater mixing in the coastal waters, due to the greater movements and turbulence of the inner edge of the Labrador Current and associated coastal eddies as they pass over rough submarine topography. The downward mixing and transfer of heat below sill depth within the fjord is, as may be expected, much more restricted and is far less at BD-33 which lies inside of a 31-m. sill.

There are small temperature inversions at BD-26 and within the mouth of the fjord at BD-27 and BD-28, indicating a more vigorous exchange and mixing

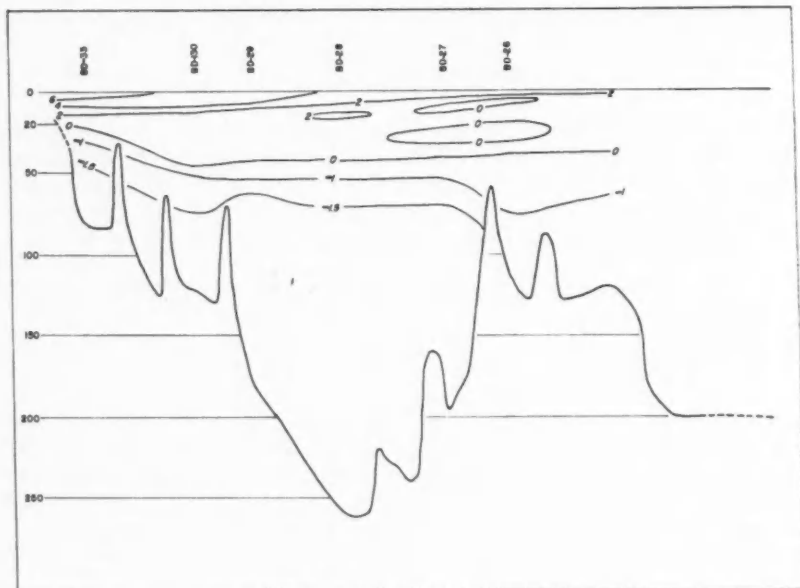


Figure 2. TEMPERATURE $^{\circ}\text{C}.$, July 9-10, 1954.

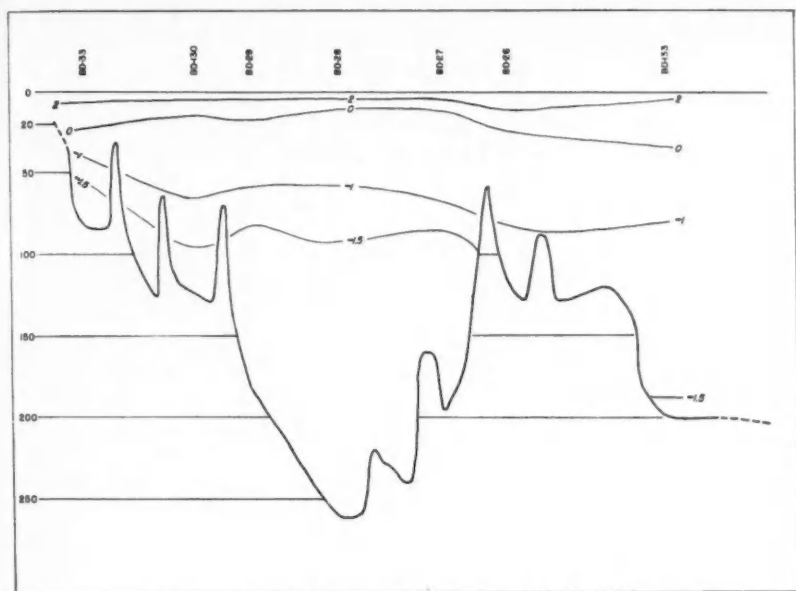


Figure 3. TEMPERATURE °C., August 11-12, 1954.

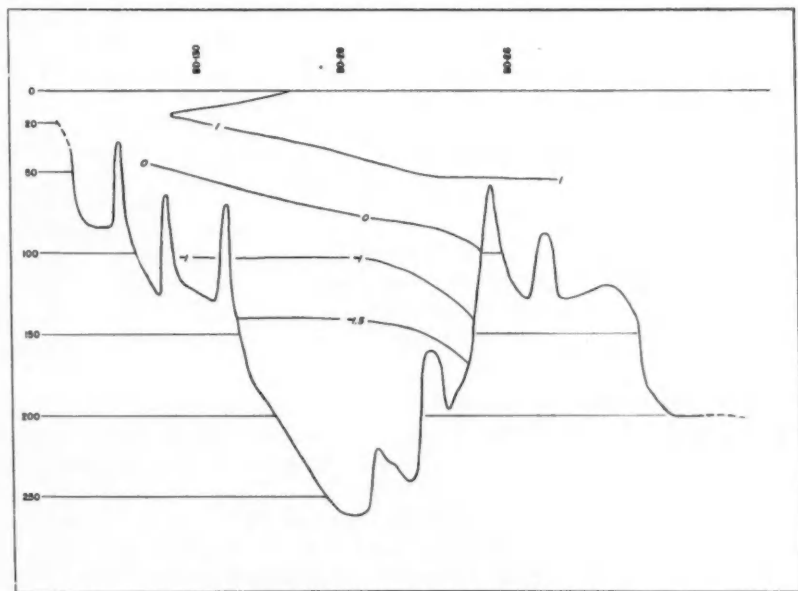


Figure 4. TEMPERATURE °C., October 15-26, 1954.

in this area than in the inner part of the fjord. However, the BT observations on July 15 taken at and near BD-130 show a large temperature inversion between 20 and 40 m. This is likely the result of the northeast storm of July 13-14 which filled the fjord with ice for a distance of 25 miles. The cooling effect of this ice was apparently small as quantitative heat calculations from the July 15 BT showed in fact a continued addition of heat (see below).

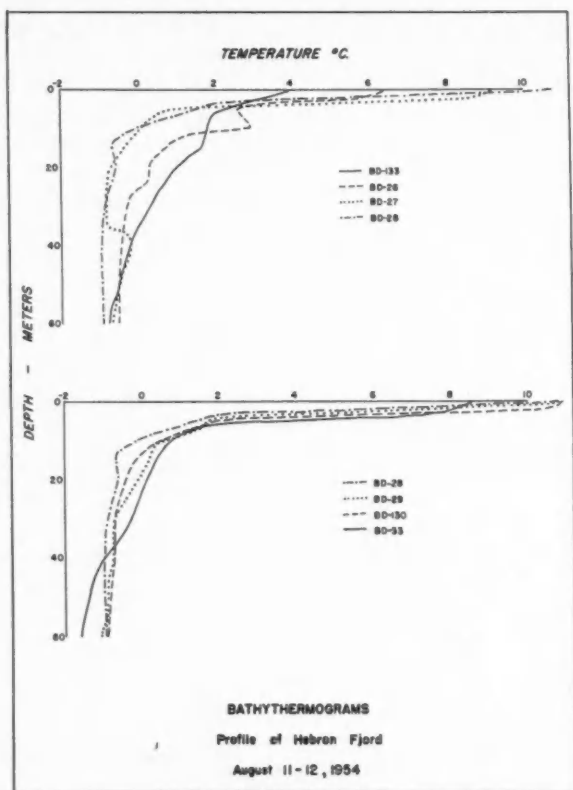


Figure 5.

On August 12 when the last summer observations were taken, unusual and apparently anomalous conditions are noted. The very surface waters show a continued warming, and so do the very bottom layers where heat has penetrated below 100 m. However, between 5 and 50 m. a great drop in temperature can be seen. Since air temperatures and inflowing fresh water during the summer months are at all times above freezing (mean July and August temperatures are 50°F.), the only possible source of negative temperatures is the coastal water. But on August 11 at BD-26 and at BD-133 further offshore there is no evidence

of low enough temperatures above sill depth to account for this cold water mass. It can only be supposed that at some time, perhaps during early August, a mass of cold water was present at the mouth of the fjord and that the reduced temperatures within the fjord are a result of exchange with this cold water mass. By the time of the August 11 observations evidence of this cold has been removed from the waters outside by the Labrador and coastal currents. The introduction

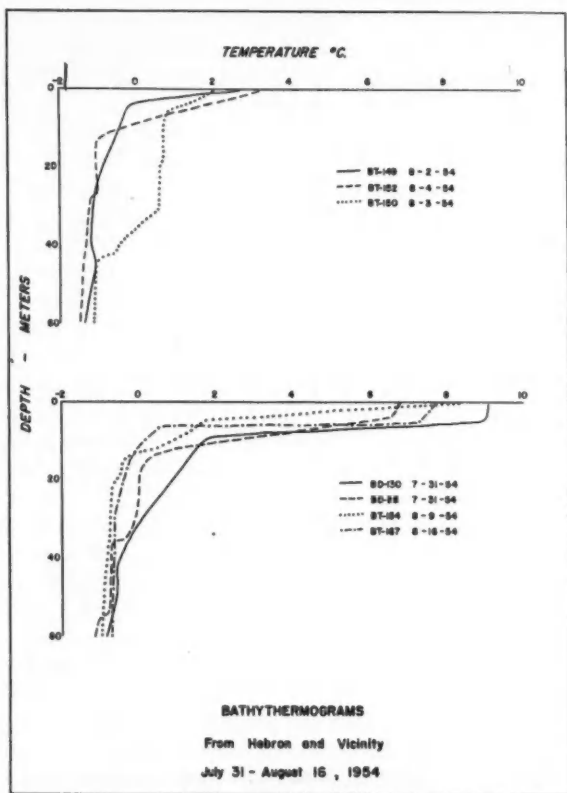


Figure 6.

of this cold water was quite rapid, and the re-establishment of what might be termed "normal conditions" (as indicated by the August 11 observations at BD-26) appears to have been equally rapid.

The BT traces down to 60 m. for the seven stations of the August 11-12 profile are given as Figure 5. These illustrate clearly the nature and extent of this cold water mass that has penetrated the fjord. The offshore station, BD-133, shows no evidence of the cold water, and there is only slight evidence at BD-26 outside the mouth of the fjord. At BD-27 and BD-28 the upper layers are

markedly colder than outside the fjord. BD-29 is similar in character but not as cold as BD-28. The same may be observed at BD-130 and BD-33, with the upper layers of each slightly warmer than the next station just outside. At BD-33 to 40- to 60-m. layer is, however, somewhat colder (about $0.5^{\circ}\text{C}.$) than at BD-130, a result of the 31-m. sill between the two stations. Thus in the process of exchange between the waters of the fjord and the coastal water, the cold water mass has been progressively tempered in penetrating the fjord. At the time of these observations its removal by exchange with the coastal water was taking place.

Various BT records from late July and the first two weeks of August are compared in Figure 6. BT-149 was taken August 2 about 2 miles WSW. of Fish Island and indicates the presence of a mass of cold water from 5 m. down. BT-152 was taken in the same place 2 days later, and the cold water mass was still present but surface warming has lowered the $0^{\circ}\text{C}.$ point from 5 m. to 10 m., while the layers immediately beneath still contain water below $-1.0^{\circ}\text{C}.$ On the day between these observations (August 3) BT-150 was taken in conjunction with the occupation of BD-133 located approximately 10 miles farther offshore, and the cold water does not extend out this far. Shown also are the July 31 BT traces for BD-130 and BD-28 in the fjord. The cold water mass at this time has started to penetrate the fjord, as water of $0^{\circ}\text{C}.$ may be noted below 15 m. at BD-28. The cold mass has not yet reached to BD-130. BT-154 was taken in Napartok to the south of Hebron on August 9, and by this time the cold water had to a certain extent penetrated this fjord. BT-167 taken August 16 in Mugford Tickle shows the remnant of the cold water mass at this time located 30 miles to the south of the Hebron area.

These BT records show that the cold water mass which so markedly influenced the fjord temperature structure at the time of the August 11-12 observations was very limited in size and passed quite rapidly from north to south off the entrance to Hebron fjord during the last few days of July and the first few days of August at a rate of approximately 2 miles per day.

Observations taken between October 15-26 show that autumnal cooling of the surface layers had begun, especially in the inner part of the fjord where the surface waters were practically at the freezing point and slob ice was observed along the shores. However, the maximum results of summer warming can now be noted in the intermediate and bottom layers. Outside the fjord negative temperatures have disappeared completely. Heat has penetrated to the very bottom water of the fjord as shown by the change of temperature at 250 m. at BD-28 from $-1.76^{\circ}\text{C}.$ in August to $-1.68^{\circ}\text{C}.$ in October.

In order to show more clearly the effects and magnitude of the annual thermal regime, computations of the quantities of heat in a column of water of 1 cm.^2 cross-section at stations BD-26, BD-28 and BD-130⁶ are given in Table

⁶Actually BD-30, located several miles further in the fjord, was occupied on April 7. Under the virtually isothermal and isohaline conditions of winter data from BD-30 and BD-130 may be considered identical. On several occasions in this paper, the April data from BD-30 have been compared with summer and fall data from BD-130.

III. The computation used is $Q = T \times c_p \times \rho_{s, v, p} \times h$ where Q is the heat in gram-calories, T is the average temperature, c_p is the specific heat, $\rho_{s, v, p}$ is the density in situ, and h the height of the column. The quantity of heat is shown for 0 to 50 m., which level lies entirely above the sill and will have free exchange with the coastal water; for 50 to 100 m., which level lies for the most part below sill depth; and for the total column 0 to 100 m. Below 100 m. the changes are quite small.

TABLE III.—Heat (in gram-calories) of a column of water one square centimetre in cross-section at various stations, 1954.

Depth <i>m.</i>	BD-26					
0-50	March 26	July 10		Aug. 11	Oct. 15	
50-100	-8,608	446		3,793	6,647	
0-100	-8,625	-4,844		-3,489	3,533	
	-17,233	-4,398		304	10,180	
BD-28						
0-50	March 29	July 10		Aug. 12	Oct. 18	
50-100	-8,470	4,317		42	6,053	
0-100	-8,481	-6,791		-5,820	969	
	-16,951	-2,474		-5,778	7,022	
BD-130						
0-50	April 7	July 9	July 15	July 31	Aug. 12	Oct. 26
50-100	-8,517	7,491	10,064	8,476	1,500	2,166
0-100	-8,481	-7,510	-5,959	-5,815	-5,819	-1,453
	-16,998	-19	4,105	2,661	-4,319	713

Between March and July in the 0- to 50-m. level the greatest warming has taken place at BD-130 and the least at BD-26, while the opposite is true for the 50- to 100-m. level. In the total column the greatest heat increase in this period is at BD-130. This may be accounted for by the warmer climatic conditions within the fjord and that by July the inflow of fresh water is likely above 0°C., whereas at BD-26 the fresh water is largely from melting ice at 0°C. and the large ice cover offshore inhibits heat transfer from the atmosphere. Thus in July heat is being added more rapidly to the waters in the fjord than to the coastal waters and heat is being transferred above sill depth from the fjord to the coastal water through the processes of exchange.

The quantitative heat determinations for the August 11-12 observations show that the cooling of the intermediate layers is not possible by heat transfer with the atmosphere but must be caused by external exchange since there has been a considerable net loss of heat by the water mass in the fjord. As in July, BD-130 remains warmer than BD-28 but there is less difference. The cold water source has passed by BD-26 where it would appear that only a progressive summer warming has taken place.

After October 15 heat is being lost at the surface and at or just prior to this time of year the maximum warming is attained. In the 0- to 50-m. level there appears to be progressively less heat from BD-26 toward BD-130, but this might be due to the fact that BD-26 was occupied on October 15, while BD-28 was occupied on October 18, and BD-130 on October 26. At this time rapid cooling

was taking place and ice was forming close to shore near BD-130. The water from 50 to 100 m. as well as the total 0- to 100-m. column is in every case warmer than in August, but considerably more heat is found in the coastal water than in the fjord water.

2. SALINITY

Longitudinal profiles of Hebron Fjord showing the distribution of salinity in ‰ for the times of observation in July, August, and October 1954 are given in Figures 7, 8, and 9. During the winter season virtually isohaline conditions prevail in the coastal water and within the fjord. As long as ice formation is in progress as well as the continuing exchange with the slightly more saline water from outside with the fjord by tidal action, salting of the fjord will continue.

When spring thaw commences, which is estimated as beginning about May 15, the snow and ice melt very rapidly, and within a relatively short period of time a large quantity of fresh water is introduced into the fjord. As this fresh water enters the upper layers, the convection of winter ceases immediately, and a stable density gradient is established.

By July 9 and 10 when the first observations of the summer were taken, the surface layers have freshened as deep as 80 to 100 m. while the large mass of bottom water remains largely unaffected. In Figure 7 the sloping of the 32.0 and 32.5‰ isohalines shows a greater downward mixing in the coastal and outer fjord water than in the inner. This confirms the evidence of the thermal regime

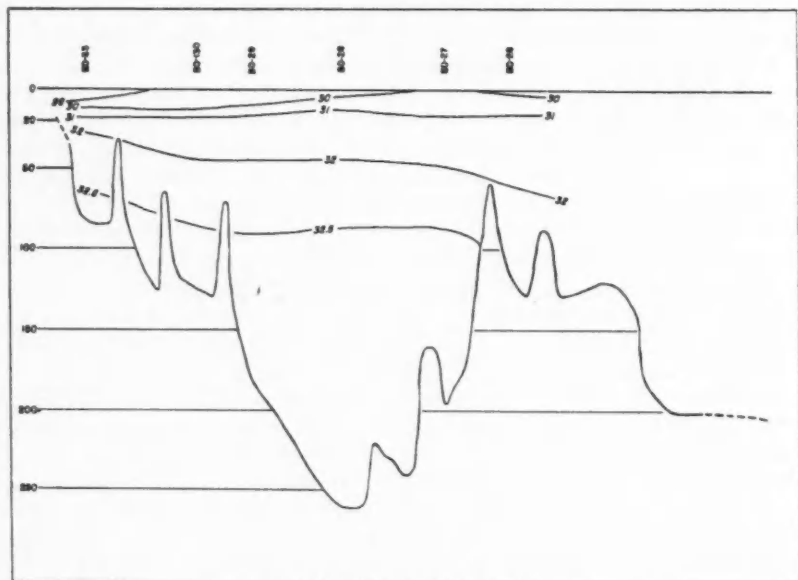


Figure 7. SALINITY ‰, July 9-10, 1954.

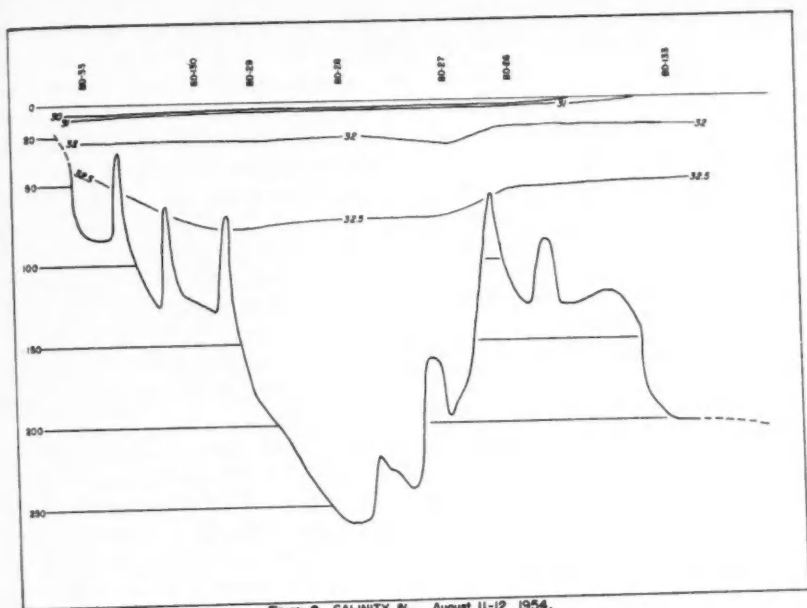


Figure 8. SALINITY ‰, August 11-12, 1954.

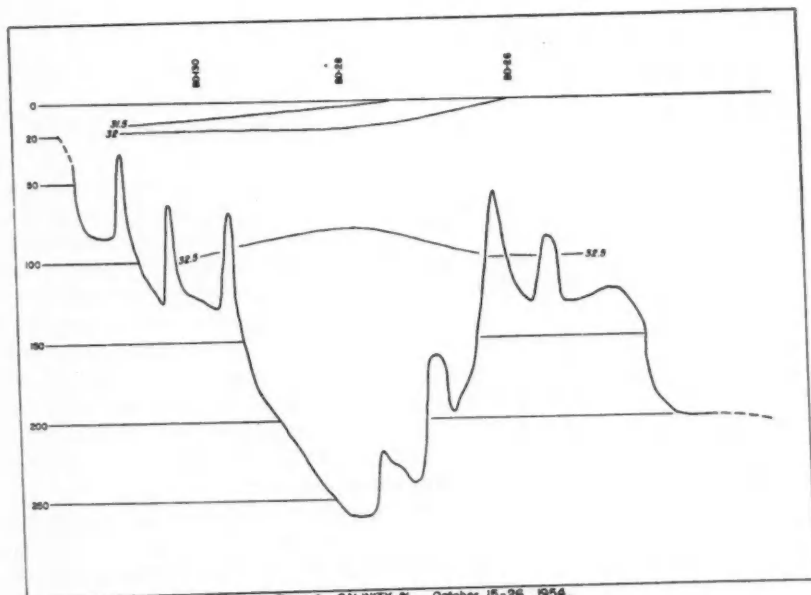


Figure 9. SALINITY ‰, October 15-26, 1954.

that there is greater turbulence and mixing in the coastal water likely due to the Labrador and associated coastal currents passing over the rough submarine topography of the continental shelf. More stable conditions and less vertical mixing prevail within the confines of the fjord. The transport of this more thoroughly mixed water into the fjord by tidal action can be seen by the progressively more stable stratification toward the inner part of the fjord.

As the summer progresses marked salting takes place in all but the very surface layers, particularly the intermediate layers above sill depth. The quantity of fresh water in the fjord responds to the volume inflow of fresh water, which by August is markedly less than the spring freshet effect noticeable in July. This salting is brought about by exchange with the coastal water and may be associated with the inflow of very cold water between observations noted previously. The observations at BD-130 taken July 31 show that an even greater freshening has taken place than earlier in July, so this sharp salting of the fjord must have been rapidly accomplished in the early days of August.

The October salinity profile (Fig. 9) shows a sharp salting of the 0- to 5-m. level due to the decreased run-off during the fall, and a continued slight freshening of the layers below sill depth due to the continued downward mixing of the comparatively fresher waters. The intermediate water of the fjord, below 5 m. and above sill depth, is quite similar to the August condition while salting has taken place outside the fjord at BD-26. The return to midwinter isohaline and isothermal conditions is accomplished by continued autumnal cooling, the formation of ice, and exchange with the Labrador Current.

3. OXYGEN

During the summer investigations in Hebron Fjord selected water samples were analysed for dissolved oxygen content. Essentially the same pattern of oxygen distribution is noted during each summer; and only the 1954 data is presented in Figure 10 for discussion.

The over-all high oxygen content of these waters is at once apparent. Photosynthetic activity appears to be producing an abundant supply of oxygen and the water above 30 m. is largely supersaturated. The water below 30 m. contains less oxygen, but there is always at least 6.0 ml./l. both offshore and within the main body of the fjord. The evidence of a reduced oxygen supply in the 50- and 75-m. levels at BD-33, which station is located inside a 31-m. sill, shows a reduced circulation and exchange in this inner basin.

The data from 100 m., which is well below the fjord sill depth and the euphotic zone, indicate a tendency toward progressively less oxygen from the coastal water toward the inner part of the fjord. Station data from BD-28 (with the exception of 250 m.) and to a lesser degree from BD-130 indicate also a slight tendency toward oxygen depletion as the season progresses.

Lack of oxygen data at seasons other than summer prevents more than a speculation concerning the annual cycle of oxygen distribution. It can be supposed that with the warming of the lower levels of the fjord during the fall, a greater metabolic rate and concurrent oxygen consumption among the animal

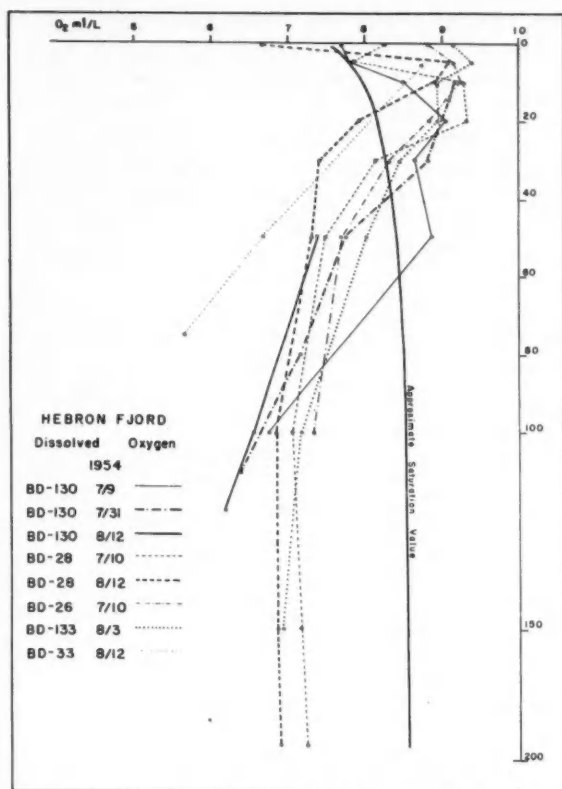


Figure 10.

populations may take place. However, at this time of year with the cooling and salting of the upper layers there is less density gradient, and exchanges and renewal are more rapid. After the formation of ice, through which the diffusion of atmospheric gases is nil (Scholander *et al.*, 1953), oxygen maintenance and renewal must take place through exchange above sill depth between the fjord and coastal waters and downward convection from the upper layers. In any case there would appear to be sufficient oxygen in all levels of Hebron Fjord throughout the year to support marine life.

4. INORGANIC PHOSPHATE (PO_4)

Determinations of inorganic phosphate content were made on samples of water from selected stations during the summers of 1952 and 1954 and are presented in Figure 11.

The 1954 data show in general an increase in phosphate with depth and it may reasonably be supposed that the reduction of phosphate in the upper layers

is associated with photosynthetic activity. In comparing the data from July with those from August a tendency is noted at each individual station toward a general increase in phosphate content above 100 m. as the summer progresses.

Quite a different pattern is shown by the 1952 data. Since these were obtained by visual comparison to colour standards rather than by EEP, great reliance in the precision of these data is not warranted. There is, however, a strong indication that the available inorganic phosphate in 1952 was considerably less than in 1954, due perhaps to a greater depletion through productivity and/or to a smaller supply by renewal.

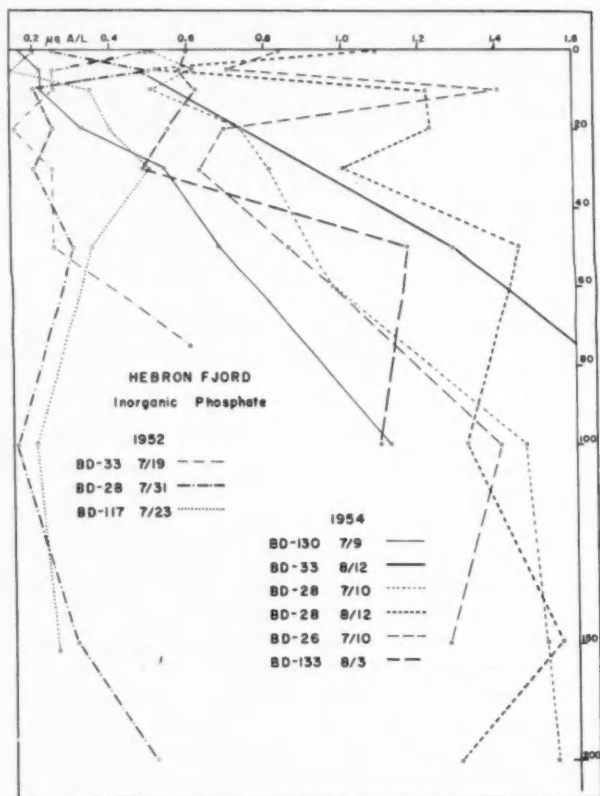


Figure 11.

5. TEMPERATURE-SALINITY RELATIONSHIPS

Temperature-salinity ($T-S$) diagrams are useful in identifying water masses and determining their relationships. The uniform isothermal and isohaline conditions during winter in Hebron Fjord form a single point on the $T-S$ diagram, which shows that a single uniform mass of water of the character of the Labrador

Current prevails at this season. This point on the diagram may vary from year to year within relatively narrow limits dependent on the Labrador Current, which is the controlling factor in the determination of the winter structure of Hebron Fjord.

The T - S relationships as observed in Hebron Fjord during the summer and fall of 1954 are given in Figures 12, 13, and 14. For simplification, observations showing extreme freshening and warming of the surface have been omitted.

In the course of the summer fresh water is added to the fjord. This fresh water must enter first at a temperature of 0°C . and later at temperatures as high

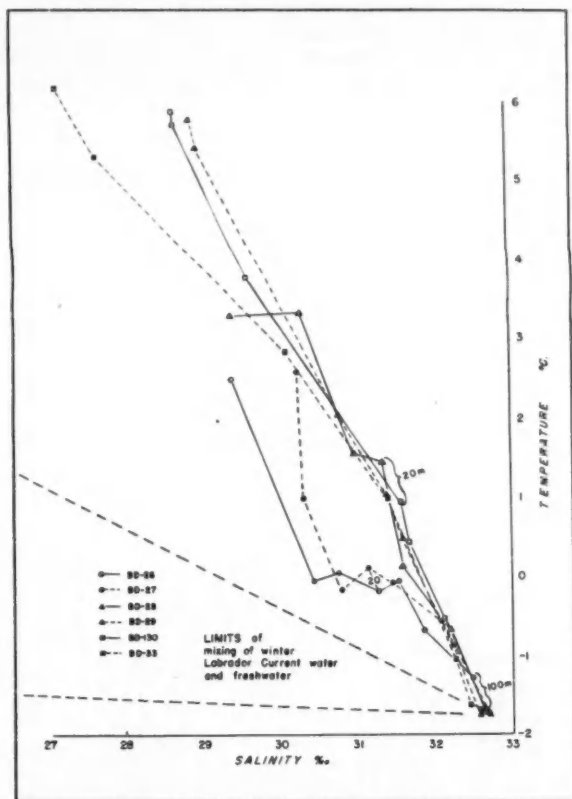


Figure 12. T - S DIAGRAM, July 9-10, 1954.

as 10 to 15°C . If the water in the fjord were only a result of the mixing of this fresh water with the Labrador Current water of winter, the T - S plot would lie within the limits indicated in Figure 12. The actual plot is more upright, indicating the absorption and downward transfer of heat in the Labrador Current, coastal waters, and within the body of the fjord during summer.

The influence of the ice cover on this downward transfer of heat can be seen from the July diagram (Fig. 12) in which BD-26 and BD-27, just offshore and within the mouth of the fjord, show a freshening with little warming, largely from melting ice, while in the inner part of the fjord much greater warming has taken place. At the time of the July observations, BD-33, BD-130, and BD-29 were all ice-free; scattered ice lay at BD-28, and BD-27 and BD-26 had 0.5 to 0.8 ice cover.

At the time of the August observations (Fig. 13) a decided salting and a continued warming has taken place in the coastal water where similar conditions exist at BD-26 and BD-133, some 10 miles further offshore. Relationships within the fjord are only slightly changed from those of July, which may be due in part to the influx of cold water noted at this time. From the T - S diagram (Fig. 13) we can determine more completely the character of this cold water mass. The temperature of the mass before it entered the fjord was -1.2 to

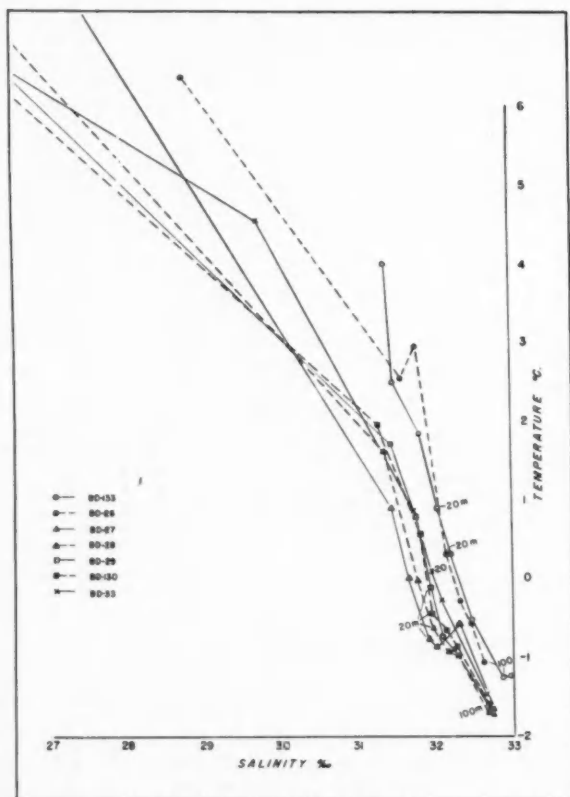


Figure 13. T - S DIAGRAM, August 11-12, 1954.

-1.3°C . (Fig. 6); and as it was coastal water, the salinity must have been 32.70 to 32.80‰.

The largest change in the character of the water masses occurs in late summer and fall, by which time all ice has melted, land drainage decreased, and surface cooling begun. At BD-130 the surface layers have cooled significantly to temperatures lower than the underlying layers where summer heat is still trapped. While the cooling and salting of the upper layers is taking place a continued slow reflection of summer warming and freshening in the bottom layers may be noted. As a result of the fall processes the water becomes more uniform, the density gradient becomes weaker and there is greater possibility of downward transport by turbulence. This can be seen in the continued freshening and warming of the bottom layers at this season. The changes in the very bottom layers, however, are of relatively little magnitude and virtually stable conditions prevail throughout the annual cycle.

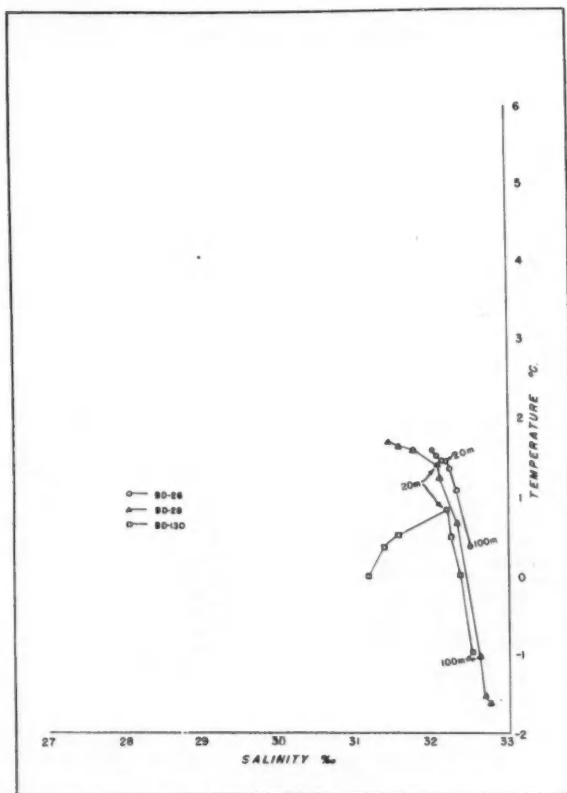


Figure 14. T-S DIAGRAM, October 15-26, 1954.

The T - S relationships show that in the course of the annual cycle the character of the water undergoes a considerable change. In the coastal waters the freshening takes place in advance of the warming while in the late summer and fall salting precedes the cooling. The same process occurs within the fjord, but varies within narrower limits. The late summer and fall changes show a lag of the fjord water in attaining through exchange the character of the coastal water. This, together with the rapid influx of the cold water mass in August, points out that conditions within the fjord are determined to a large degree by the conditions in the coastal waters. Finally the uniformity of the bottom water of the fjord with little variation throughout the annual cycle is emphasized in comparison to the more substantial warming that occurs in the bottom layers offshore.

So far only the seasonal cycle in 1954 has been considered. In Figure 15 are plotted the T - S relationships for the 1949 and 1952 observations together with the August 1954 observations, which were selected as being most nearly comparable. To show the year-to-year relationships more clearly a line plot of the average coastal and main fjord relationships is given (Fig. 16).

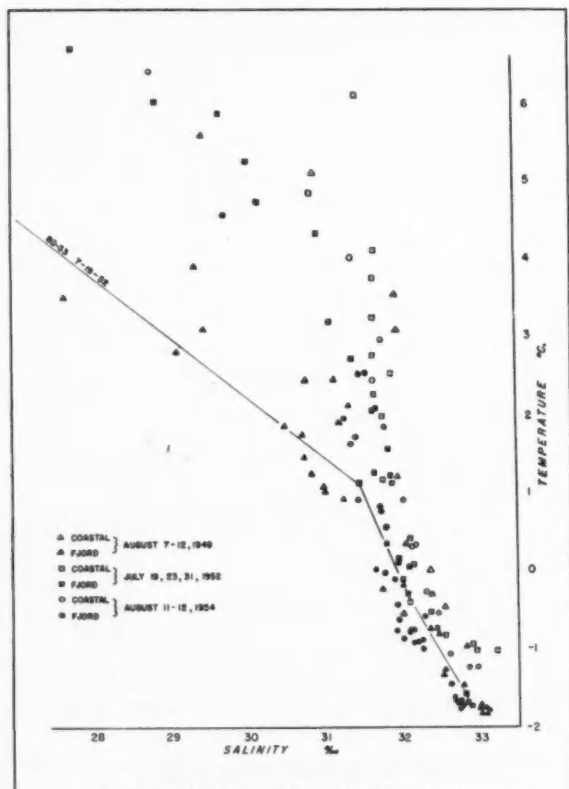


Figure 15. T - S COMPARISON, 1949, 1952, 1954.

One striking feature is the midsummer uniformity of the coastal water, with the exception of the surface where variations are bound to occur. A greater variation is noted within the fjord. The same conditions as described above in the seasonal analysis of the 1954 data seem to exist in 1949 and 1952. The coastal water in the upper layers is generally more saline. A greater difference between the coastal and fjord water in 1949 than in the other years is noted. In 1952 the fjord water is almost approaching the coastal water in character, which may be explained by the fact that the fjord observations were taken a week later, and as indicated in the seasonal cycle of 1954 the fjord water tends to attain the character of the coastal water. The single occupation of BD-33 on 19 July 1952 showed conditions much fresher and more characteristic of early summer (Fig. 15).

The 1952 coastal water observations were made at least 2 weeks earlier in the summer than were the observations in either 1949 or 1954, and the fjord water observations were made 8 to 12 days earlier. The fact that the 1952 relationships both within the fjord and in the coastal water are approaching a late

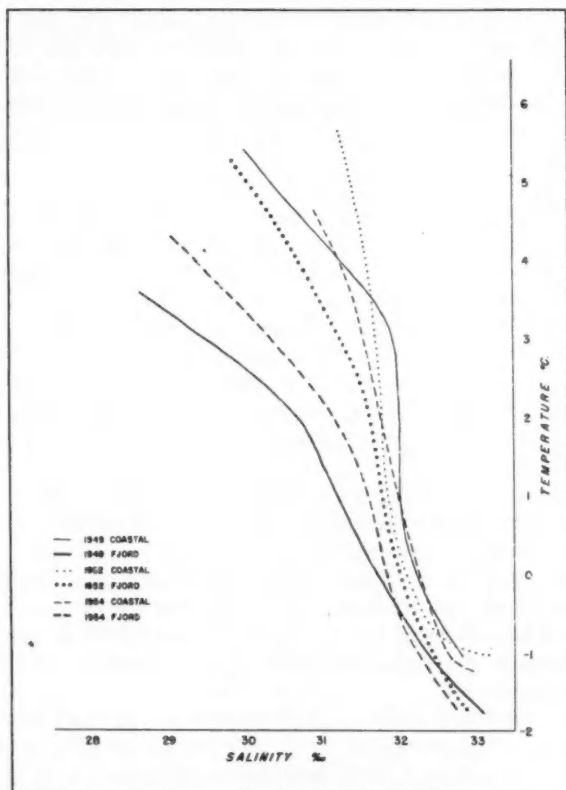


Figure 16. T-S COMPARISON, 1949, 1952, 1954.

summer condition at the earlier date suggests a more advanced season in 1952. This is borne out by the rather fine weather, early departure of ice, and the relatively little precipitation in 1952.

In the deeper layers there appears to be no specific relationship between the bottom water (below 100 m.) within the fjord and in the coastal waters. In each case slightly different T - S relationships are noted. The principal difference is the distinct warming of the very bottom water offshore while the bottom water within the fjord shows no change. Only very slowly does the summer heat and freshening penetrate to the levels below 100 m. inside the fjord, where no significant change is noted until late fall, at which time, because of the salting and cooling of the surface layers and the weaker density gradient, these effects can more readily be transported downward. That these effects are transported downward is clearly shown by the progressive freshening of the bottom water over the period from 1949-1954 (see Long-term Trends below). Unless the stable density gradient is overcome this freshening could not have taken place and the more saline water of an earlier year would have been trapped in the bottom with ensuing stagnation, of which there is no evidence.

It is at the same time quite evident from the March 1954 observations, with virtual isothermal and isohaline conditions within the fjord and coastal waters, that the character of the bottom water is determined by the conditions of the Labrador Current during the winter season and that this character is for all practical purposes retained well along toward late summer.

6. LONG-TERM TRENDS

It is well known that the Arctic regions have been undergoing a period of climatic and oceanic warming (Dunbar, 1951; Jensen, 1939; Zubov, 1948). Off West Greenland water temperatures have risen 1.0 to 2.0°C. since 1920; but trends of such magnitude have not been measured in the Canadian eastern Arctic. Bailey and Hachey (1951a) reported an increasing Atlantic influence in Hudson Bay where between 1930 and 1948 there appeared to be a rise in temperature of the bottom waters of approximately 0.4°C. and an increase in salinity of 0.50‰. In comparing the 1949 *Blue Dolphin* data from 50 m. and below with corresponding 1926 *Chance* data, no apparent change seemed to have taken place (Nutt, 1953).

However, with the addition of the *Blue Dolphin* data of 1952 and 1954 and a better understanding of the oceanographic processes involved, a decided trend of small magnitude may now clearly be seen.

Observations in Hebron Fjord in 1954 show that by August the summer influences of warming and freshening have reached well below 50 m. These upper layers will be influenced by the amount and character of the run-off, the climatic conditions of the particular season, and the vagaries of the Labrador Current and coastal eddies.

However, in the lower levels seasonal changes are of small magnitude; and it is only in autumn that any significant changes can be noted below 100 m. The character of the very bottom layers would appear to be noticeably changed only

within the period of a full annual cycle, particularly during the winter season at which time vertical convection takes place and the entire mass of fjord and coastal water becomes uniformly isothermal and isohaline with T - S characteristics of true Arctic water of the Labrador Current. It would therefore appear that this very bottom water assumes its T - S characteristics principally during this season and that the early and midsummer observations of these lower levels represent essentially conditions that had become established during the previous winter. Since winter observations have only been made once, any analysis of longer term trends must be made from the more numerous summer data. By restricting the analysis to the lower levels only, a reasonably valid picture which will not be obscured by irregular variations during summer may be obtained.

A T - S diagram showing a comparison of the 1926 *Chance*, and 1949, 1952, and 1954 *Blue Dolphin* data from 100 m. and below, is presented as Figure 17, and the T - S trends are summarized as follows:

Period	No. of years	Total warming °C.	Warming per year °C.	Total freshening ‰	Freshening per year ‰
1929-49	23	0.03	0.0012	0.12	0.005
1949-52	3	0.05	0.017	0.24	0.08
1952-54	2	0.03	0.015	0.10	0.05

It must be pointed out that the *Chance* data are from Nachvak Fjord, while the *Blue Dolphin* data are from Hebron Fjord. Hebron and Nachvak Fjords are

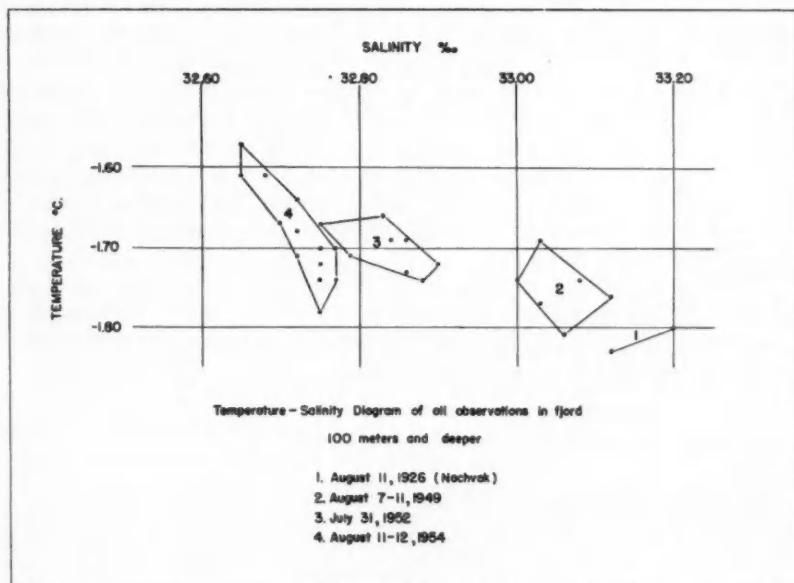


Figure 17. LONG-TERM TRENDS.

within 60 miles of each other and of quite similar bathymetric structure. It is believed that for the purposes of this paper a comparison of these data can reasonably be made.

A very slight warming trend and particularly a trend toward freshening can be readily noted. These trends would seem to be taking place at a more rapid rate in recent years during the period of the *Blue Dolphin* observations.

The 1926-49 trend is barely significant and the average per year rate of change of little meaning. However, from 1949 to 1954 a definite and regular trend is evident.

The coastal waters of Labrador lie on the "tail end" of the Arctic side of the over-all Atlantic-Arctic circulation. It is possible that the significant warming noted in the waters off West Greenland and elsewhere in the waters of the Northern Hemisphere is only in very recent years being felt in the Canadian waters of Labrador, and that the comparatively slight but definite trend, noted since 1949, is the beginning of a greater change as the Atlantic-Arctic circulation continues.

The freshening of the waters off Labrador is even more apparent. This freshening could be due to an increased annual precipitation with attendant increased land drainage. However, since the condition of the bottom water is determined largely during the winter period of vertical convection and exchange, when run-off plays no part, another explanation seems to be demanded.

A correlation with the recent changes in the Arctic Ocean is suggested. The decrease in general ice thickness, area of sea-ice cover, as well as the decrease in the thickness of the surface layer of Arctic water (Zubov, 1948) would result in the removal of a large quantity of fresh or low-salinity water from the Arctic Ocean and replacement by Atlantic water of higher salinity. This removal of fresh water would have to take place through the East Greenland and Canadian Currents, and the inner band of the Labrador Current. Freshening of the water of these currents tends to create a greater dynamic urge and a consequent greater volume of transport of Arctic water. It is also suggested that perhaps the Arctic water transported along the Labrador coast has served as the inhibiting restraint on any significant warming of the water (except summer processes) such as have occurred elsewhere in the Arctic.

A correlation between the increasing salinity in the bottom water of Hudson Bay and the decreasing salinity in the waters of the Labrador coast and fjords has not been established. Future investigations in Labrador and particularly in Hudson Bay are needed to clarify this problem.

III. ICE

Of all the oceanographic phenomena in Arctic and sub-Arctic areas, ice formation has perhaps the greatest practical significance, due to the limitations it imposes on navigation, aircraft landings, and surface transport. From December until June on the average Hebron Fjord is ice covered, which has several effects on the winter oceanographic processes.

Autumnal cooling and ice formation result in thermo-haline convection. Cooling and salting begins at the surface and progresses downward. The formation of ice has the actual net effect of adding salt to the water beneath, while the ice itself stores at the surface a substantial volume of fresh water to be returned to the fjord during spring thaw and break-up.

Ice thicknesses observed in Hebron Fjord during March and April 1954 were as follows:

Location	Ice thickness	Snow cover
	<i>m.</i>	<i>m.</i>
BD-26	0.41	0
Hebron Harbour	1.30	0.36
In fjord just off harbour	1.14	0.30
BD-28	0.84	0.25-0.30
BD-130	1.19	0.61

Essentially the same thicknesses were measured in the spring of 1955.⁶

Except for BD-26, where the station was purposely made in a newly frozen lead to lessen the work of cutting through the ice, the thicknesses are fairly representative of ice formation that might be expected with the greater amounts close to shore and in the inner fjord. In general one might estimate that an average of 1 m. of ice forms during a winter.

By computing the effects of the thermo-haline convection resulting from autumnal cooling and ice formation on the physical structure of the water it is possible to gain further insight into the oceanographic processes of winter. The method of Defant (1949) is followed except that for convenience σ_t is used instead of specific volume and the ice formed is assumed to have a salinity of 5‰. The method of computation is outlined briefly. A water column of 1 cm.² cross-section is divided into horizontal layers and the average temperature, salinity, and density of each layer are determined from the station data. As cooling takes place at the surface the upper layer becomes more dense until it has attained the density of the layer beneath, when the two layers mix. The point at which this takes place is determined from a T - S diagram with σ_t lines superimposed. The temperatures before and after mixing are then known; and from the temperature difference the quantity of heat Q_i lost due to atmospheric cooling may then be computed. The salinity of the mixed layer corresponds to the average of the salinities of the two separate layers before mixing.

One may then proceed to combine the third layer with the first two and so on. But dependent on the physical structure of the water, a point may be reached where the surface layer when cooled to its freezing point is not of a sufficient density to continue the process of thermal convection. Here ice forms. But as ice forms the average salinity of the column will increase because of this ice formation, and convection will in fact continue. By referring to the T - S - σ_t diagram it is possible to determine the increase in salinity due to ice formation; and the thickness e of ice formed and the amount of heat Q_e lost in the formation of ice (latent heat of fusion) may be computed. The total heat lost is the sum of the heat lost in cooling the water column and the heat lost in ice formation.

⁶P. F. Scholander, personal communication.

Computations of the thermo-haline convection resulting from autumnal cooling and ice formation have been made for stations BD-26, BD-28, and BD-130 based on the October 1954 observations, and have been carried on until the thickness of the ice formed is in reasonable agreement with what might be expected or until the bottom was reached, thus: BD-26 (62 cm. of ice), convection to bottom at 120 m.; BD-28 (96 cm. of ice), convection to 90 m.; BD-130 (120 cm. of ice), convection to bottom at 120 m. The results are summarized in Table IV.

TABLE IV.—Thermo-haline convection in Hebron Fjord, October 1954.

Layer	Layer thickness (m.)	Q_t	e	Q_e	ΣQ	Σe
BD-26 October 15						
1-2	10	0.48	0.48
1-3	20	0.60	1.08
1-4	30	1.77	2.85
1-5	40	2.98	5.83
1-6	50	5.00	10.83
1-7	60	6.15	16.98
1-8	70	3.39	1.4	0.10	20.47	1.4
1-9	80	2.32	9.8	0.71	23.50	11.2
1-10	90	2.09	10.9	0.78	26.37	22.1
1-11	100	2.03	16.2	1.17	29.57	38.3
1-12	110	2.02	8.9	0.64	32.23	47.2
1-13	120	1.97	14.6	1.05	35.25	61.8
BD-28 October 18						
1-2	10	1.02	1.02
1-3	20	5.34	4.1	0.30	6.66	4.1
1-4	30	2.99	2.5	0.18	9.83	6.6
1-5	40	2.75	3.3	0.24	12.82	9.9
1-6	50	2.42	20.5	1.48	16.72	30.4
1-7	60	2.32	12.2	0.88	19.92	42.6
1-8	70	2.10	14.2	1.02	23.04	56.8
1-9	80	1.86	9.7	0.70	25.60	66.5
1-10	90	1.40	29.1	2.10	29.10	95.6
BD-130 October 26						
1-2	10	1.93	0.8	0.06	1.99	0.8
1-3	20	2.34	10.8	0.78	5.11	11.6
1-4	30	2.35	24.6	1.77	9.23	36.2
1-5	40	2.05	6.5	0.47	11.75	42.7
1-6	50	1.80	8.1	0.58	14.13	50.8
1-7	60	1.69	2.4	0.17	15.99	53.2
1-8	70	1.76	5.7	0.41	18.16	58.9
1-9	80	1.54	6.5	0.47	20.17	65.4
1-10	90	1.31	14.6	1.05	22.53	80.0
1-11	100	0.97	12.1	0.87	24.37	92.1
1-12	110	0.64	13.3	0.96	25.97	105.4
1-13	120	0.58	14.5	1.04	27.59	119.9

Q_t = Heat lost to atmosphere in kg-cal./cm.²

Q_e = Heat lost to ice formation in kg-cal./cm.² (latent heat of fusion).

e = Ice thickness in cm.

The prediction of the date of freeze-up is of considerable practical importance. From these computations the quantity of heat that must be lost prior to ice formation can be determined. If we assume for the moment that from the date of observation the rate of effective heat loss to the atmosphere is 0.1

g-cal./cm.²/min., it is then possible to obtain in advance some notion of the date of freeze-up. Applying this to the October data from Hebron Fjord, we have:

Station	Heat loss to ice formation	Date of observation	Number of days to freeze-up	Date of freeze-up
	<i>kg-cal./cm.²</i>			
BD-26	20.37	Oct. 15, 1954	141	Mar. 5, 1955
BD-28	6.36	Oct. 18, 1954	44	Dec. 1, 1954
BD-130	1.93	Oct. 26, 1954	13	Nov. 8, 1954

From this it is possible to conclude that the inner fjords and bays of Labrador will freeze over first and the ice will gradually spread seaward. This is confirmed by local observation and knowledge. In 1954 slob ice was making along the shores of the inner fjord on October 26 at the time of occupation of BD-130, while the fjord, off the village of Hebron near its mouth, was reported to have frozen over on December 14. Of particular significance is the low "ice potential" at BD-26 in the coastal water as compared with the main body of the fjord. Ice is known to form here at an earlier date than that shown by the computations. In March 1954 off shore from the fjord, ice was forming rapidly in any open water, and the hydrographic structure was clearly favourable. Hence in the coastal waters in addition to convection resulting from atmospheric cooling some change in the physical structure of the water must also occur to hasten the ice formation.

With the relatively stable conditions that appear to exist in Hebron Fjord, particularly during the winter regime, it would seem reasonable for the purposes of this study to assume a return during the spring of 1955 to the same water structure and ice cover observed in 1954. It is then possible to compare the results predicted by the process of thermo-haline convection with the approximate conditions to be found.

Temperatures resulting from the convection are at the freezing point and in close agreement with the observed conditions; but in the salinity structure there is substantial disagreement. In order to obtain the observed salinity of approximately 32.75‰ it would be necessary to form approximately 2 m. of ice. This would seem quite unlikely in view of the none-too-severe winter climate of Labrador, and certainly untenable in view of the measured thicknesses in March and April, 1954 and 1955. It is thus apparent that the increase in salinity during the winter is not brought about alone by ice formation but must be due in part to the exchange with the Labrador Current and coastal waters. A summary of the winter haline processes as applied to a column of water of 1 cm.² cross-section from the surface to the depth of computed convection is presented in Table V.

Greater ice growth and consequently a greater increase in salinity due to ice formation appears to be taking place progressively from the coastal water toward the inner part of the fjord, while conversely the effects on the salinity structure through the process of exchange appear to be of greater magnitude in the coastal water and progressively less within the fjord. The above breakdown

TABLE V.—Summary of winter haline processes in Hebron Fjord.

	BD-26	BD-28	BD-130
Average October salinity of water column, ‰	32.33	32.29	32.28
Average salinity of ice formed, ‰	5.00	5.00	5.00
Ice thickness computed as result of thermo-haline convection, <i>m.</i>	0.62	0.95	1.20
Ice thickness observed, <i>m.</i>	..	0.84	1.19
Depth to which convection computations carried, <i>m.</i>	120	90	120
Average salinity computed as result of ice formation, ‰	32.46	32.47	32.53
Observed March–April salinity, ‰	32.76	32.75	32.73
Increase in average salinity due to computed ice formation, ‰	0.13	0.18	0.25
Increase in average salinity due to exchange, ‰	0.30	0.28	0.20
Total increase of average salinity, ‰	0.43	0.46	0.45

has been shown as two separate processes, but it is implicit that they occur simultaneously.

Let us take a closer look at the thermal processes. The atmosphere must be the primary source of cooling during the autumn until ice formation commences. Atmospheric cooling most certainly accounts for the heat lost (latent heat of fusion) in the actual ice growth. After an ice cover has formed, atmospheric cooling of the water will be considerably reduced; and the process of exchange may play a greater part in further heat loss especially in the lower layers where the heat could not be removed except by exchange.

As the winter processes continue after ice begins to form, it may not be unreasonable to assume that, as the temperature and salinity approach the mid-winter equilibrium, the heat losses during this period due to ice formation and to exchange are proportional to the increases of average salinity due to these causes.

At the same time we are interested in the rates of heat loss. It is probable that the winter conditions of equilibrium are reached in early March. Uniform hydrographic conditions were observed in March 1954, and further increases in ice thickness will for all practical purposes be negligible. For purposes of computation it is assumed that the heat has been removed until some time in March, over a period of 150 days. Thus by dividing the heat losses by the period of time involved it is possible to determine the effective rate of heat loss.

In Table VI are summarized the winter thermal processes in Hebron Fjord as applied to a column of water of 1 cm.² cross-section extending from the surface to the depth of computed convection. In the case of BD-26 the picture is obscured and complicated by the arrival during winter of the pack ice and its continual breaking up and refreezing. Therefore in this case only the totals are given, with no attempt at a breakdown.

It can be seen that in addition to the formation of ice and the associated convection, exchange plays a significant part in the winter oceanographic processes and is the ultimate determining factor in the oceanographic conditions. As we have seen from an analysis of the summer temperature regime, transports of a considerable magnitude can take place quite rapidly. Hence any long term prognosis of freeze-up date and ice thicknesses by computations of thermo-haline

TABLE VI.—Summary of winter thermal processes in Hebron Fjord.

	BD-26	BD-28	BD-130
Heat losses to atmosphere:			
Before ice formation, <i>kg-cal./cm.²</i>	..	6.36	1.93
Actual ice formation, <i>kg-cal./cm.²</i>	..	6.90	8.63
Proportion after ice formation, <i>kg-cal./cm.²</i>	..	6.20	9.26
Total heat losses to atmosphere, <i>kg-cal./cm.²</i>	..	19.46	19.82
Proportion to exchange after ice formation, <i>kg-cal.</i>	..	9.64	7.77
Total heat loss, <i>kg-cal.</i>	35.25	29.10*	27.59
Average rate of loss to atmosphere, <i>g-cal./cm.²/min.</i>	..	0.090	0.092
Average rate of loss by exchange, <i>g-cal./min.</i>	..	0.045	0.035
Total rate of heat loss, <i>g-cal./min.</i>	0.164	0.135*	0.127

*These values only apply to the depth of computed convection. Below this depth there is an additional quantity of residual heat of 4.30 kg-cal. that must be removed by exchange. For BD-28 the total rate of heat loss from the surface to the bottom would be 0.150 g-cal./min.

convection alone is liable to certain inherent inaccuracies; and along with any such studies the problems of transport and exchange between the fjords, bays, and coastal waters must be considered. Although the method used is crude, the results suggest that it gives a reasonably valid description of the actual winter processes.

IV. EXCHANGE

Exchange in an estuary with a deep basin and sill may be divided into two basically different parts; that taking place above the sill and that of the deeper layers. In Hebron Fjord exchange above the sill is essentially horizontal flows motivated by tidal action and fresh water transports. Below the sill exchange takes place by vertical convection in winter and during the other seasons, for the most part by turbulence. Although these two are related, we will discuss certain aspects of exchange primarily above the sill in this section and vertical mixing below sill depth in the following section.

By means of fresh-water fractions the actual quantities of fresh water in the various levels of the fjord for the times of observation in 1954 have been calculated and are presented in Table VII. The volumes of the levels used were determined by planimetry and the average salinity was calculated from the station data applied to appropriate segments within these levels. The fresh-water fraction (FWF) of each segment was obtained by the formula:

$$\text{FWF} = \frac{S_B - S_A}{S_B}$$

where S_A equals the base salinity of the source water and S_B equals the average observed salinity of the water in question. A base salinity of 32.79‰ was used for these calculations, which was the highest salinity observed in or just outside the fjord in 1954. By multiplying the FWF by the volume of each segment the actual quantity of fresh water in the segment was determined, and the total within each level obtained by summing the fresh water in each segment.

TABLE VII.—Fresh water in Hebron Fjord, 1954.

Level	March	July	August	October
m.	10 ⁶ cu. m.	10 ⁶ cu. m.	10 ⁶ cu. m.	10 ⁶ cu. m.
0-5	0.6	115.8	194.8	46.1
5-10	1.3	89.9	38.8	38.0
10-20	2.9	113.7	54.5	52.4
20-30	2.7	69.1	40.3	34.6
30-60	7.3	109.0	75.9	71.1
Vol. above sill:	14.8	497.5	404.3	242.2
60-100	6.6	29.9	31.7	43.0
100-150	4.4	13.2	5.5	14.3
150-200	2.6	6.5	2.0	4.6
200-250	1.1	2.6	0.8	0.8
Below 250	0.1	0.1	0.0	0.0
Total	29.6	549.8	444.3	304.9

From these data and the fresh water entering the fjord (Table II), the overall exchange of fresh water is summarized in Table VIII.

The total fresh water in the fjord reflects the annual cycle of the fresh-water contributions with the maximum observed fresh water in the fjord occurring in July after spring freshet. The total amount of fresh water decreases regularly throughout the late summer and fall as the fjord adjusts to the progressively reduced contributions of fresh water.

TABLE VIII.—Fresh water exchange, Hebron Fjord.

	May-July	July-Aug.	Aug.-Oct.	Oct.-Mar.
	10 ⁸ cu. m.	10 ⁸ cu. m.	10 ⁸ cu. m.	10 ⁸ cu. m.
Initial accumulation (start of period)	0.3	5.5	4.4	3.0
Fresh water added:	8.4	1.3	2.3	0.5
Total	8.7	6.8	6.7	3.5
Final accumulation (end of period)	5.5	4.4	3.0	0.3
Net fresh water exchanged	3.2	2.4	3.7	3.2
Period ^a	56 days	33 days	70 days	150 days ^b
Net exchange per day	0.057	0.073	0.053	0.021

^a The beginning of spring freshet is estimated at May 15.

^b 150 days is an arbitrary assumption of the time required for the return to isothermal and isohaline conditions of midwinter.

The change in fresh-water content of the levels below sill depth indicates that exchange is taking place with the upper levels. The intrusion during early August of the cold and more saline water mass is evident in the sharp salting of the fjord water from 5 m. to nearly the bottom, with an apparent damming up of the fresh-water contributions in the upper 5 m.

Calculations of flushing time, defined as the time necessary to renew the water within the estuary, have been made using fresh water as a tracer. For

these calculations a false bottom has been assumed at 60 m. which is approximately sill depth. Below this depth during summer exchange must overcome the stable density gradient and is of small magnitude as compared to the exchange above sill depth.

The formula $F = \frac{Q}{R}$, where Q is the total accumulated fresh water, and R is the river flow (contribution of fresh water), has been used to calculate the flushing time (F) above sill depth (60 m.) at the times of observation in July, August, and October in the following tabulation:

	9-10 July	11-12 August	18-26 October
$Q \times 10^6 \text{ m}^3$	4.98	4.04	2.42
R per day $\times 10^6 \text{ m}^3$	0.090	0.031	0.021
F , days	55	130	115

This method presupposes a "steady state." In Figure 18 the annual cycles of the daily rate of R , R_e (fresh water exchanged out of the estuary), and Q are given. Q reaches a maximum where $R = R_e$. Prior to this time $R > R_e$ and the fresh water in the fjord is increasing; after this time $R < R_e$ and it is decreasing. In either case R is changing so that an adjustment to a steady state is never achieved. The point of crossing of these two curves is interesting, for at this time the conditions of no net exchange of either fresh or salt water exist momentarily.

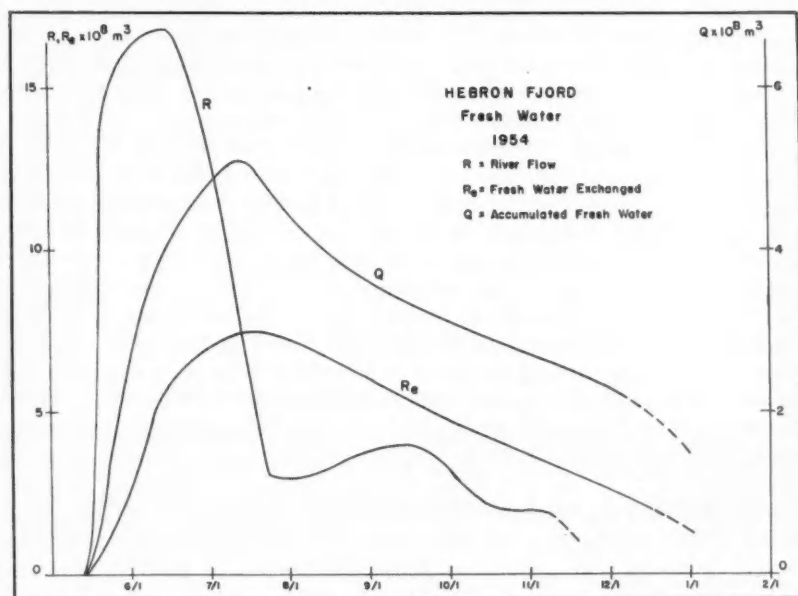


Figure 18.

Any computation of flushing time by $F = \frac{Q}{R}$ will yield too small a flushing time prior to the point where $R = R_c$, and too large a flushing time after. Therefore when $R = R_c$, the conditions of a steady state must momentarily exist. At no other time during the annual cycle is a steady state realized (except in the zero/zero relationship of midwinter).

If in such an estuary observations have not been obtained when $R = R_c$, it should be possible to solve graphically for values of Q and R at precisely this time. By so doing with the Hebron data a Q of $5.1 \times 10^8 \text{ m}^3$ and an R of $0.075 \times 10^8 \text{ m}^3$ are obtained, which yield a flushing time of 68 days. This time lies between the other values of 55 and 130 days and should be a reasonable representation of the actual flushing time. The value of 55, although obtained close to when $R = R_c$, would appear to be too rapid a flushing time. If the fjord were flushed in 55 days, a steady state would have been met or more nearly achieved during August, September or October when R is comparatively constant. This argues for perhaps an even greater flushing time than 68 days, but the present data do not permit a closer analysis.

Since it has been shown that the flushing time within a given estuary will remain constant in spite of large variations of R (Ketchum, Redfield and Ayers, 1951), we may conclude that at least during summer above sill depth the water in Hebron Fjord will be renewed regularly in a period of between two and three months.

V. VERTICAL MIXING BELOW SILL DEPTH

Exchange below sill depth must involve vertical movements, and may take place by convection and turbulence (used herein to mean eddy conductivity in the case of temperature and eddy diffusivity in the case of salinity). During winter when the water is isothermal and isohaline, exchange between the upper and lower levels occurs principally by convection. Turbulence is acting at all seasons simultaneously with the other processes, but would seem to be the dominant factor during summer when a stable density gradient must be overcome in any vertical movements. Within the body of the fjord below sill depth horizontal movements would appear to be restricted.

The source of energy for the turbulence is the tidal action and transports of fresh water through the fjord. In considering only the waters below sill depth turbulence should be greatest just at sill depth closest to the source of energy and progressively less toward the lower levels until it becomes inseparable from convection in the virtually uniform water that persists in the very bottom layers. It would therefore seem most advantageous to study the eddy coefficients for the levels at and just below sill depth during the summer season when a stable gradient exists.

From the 1954 data at station BD-130 some calculations of the "Austausch" A factor of eddy conductivity and eddy diffusivity have been made at and below sill depth at the 60-, 80- and 100-m. levels. The method of Saalen (1950) has been used:

$$\int_z^b (T_2 - T_1) dz = -\bar{A} \int_{t_1}^{t_2} \frac{\partial T}{\partial z} dt$$

$$\int_z^b (S_2 - S_1) dz = -\bar{A} \int_{t_1}^{t_2} \frac{\partial S}{\partial z} dt$$

where T_2 , S_2 , and T_1 , S_1 , are respectively the temperatures and salinities at the times t_2 and t_1 , b is the depth at bottom, z is the depth of calculation, and \bar{A} is a mean value of A during the time between t_1 and t_2 . Values for \bar{A} have been calculated over the periods between the various observations from the beginning of spring melting and the establishment of a stable density gradient (May 15) until the fall observations in October. The results are summarized in Table IX.

TABLE IX.—Calculations of eddy conductivity (\bar{A}_T) and (\bar{A}_S) diffusivity, Hebron Fjord, 1954.

Depth	\bar{A}_T				Mean
	5/15-7/9	7/9-7/31	7/31-8/12	8/12-10/26	
<i>m.</i>					<i>m.</i>
60	57	82	17	112	67
80	48	29	25	46	37
100	20	8.4	17	18.5	16
	\bar{A}_S				
	5/15-7/9	7/9-7/31	7/31-8/12	8/12-10/26	
60	111	48	(X) ^a	44	—
80	188	12	(X) ^a	32	—
100	108	(X) ^a	(X) ^a	21	—

^a Negative values representing impossible solutions (see text).

There is a large variation between the individual values in each table and a variation between the \bar{A} values obtained from temperature and from salinity. The theory implies that \bar{A}_T should equal \bar{A}_S ; however it must be pointed out that in the determination of \bar{A}_T only the transfer of a property is involved, while in the determination of \bar{A}_S an actual transfer of mass is required.

In interpreting and evaluating these data we must consider the formula itself. $\frac{\partial T}{\partial z}$ and $\frac{\partial S}{\partial z}$ are obtained from the thermogram or halogram involved.

Broadly speaking, in the course of the annual cycle $\frac{\partial T}{\partial z}$ and $\frac{\partial S}{\partial z}$ are zero at the beginning of spring freshet, increase to a maximum value during summer, and decrease again to zero during the ensuing winter. Thus regardless of the left-hand side of the equation \bar{A} will range from infinity to a minimum during summer and again approach infinity in winter.

In Hebron Fjord $\frac{\partial T}{\partial z}$ and $\frac{\partial S}{\partial z}$ are always small and difficult to determine accurately. Greater precision may be expected from the thermogram which is

obtained from a BT with reversing thermometer control, while the halogram is determined from the salinity data alone with the slope and nature of the curve determined by inference from the thermogram. The \bar{A} values obtained become extremely tenuous as $\frac{\partial T}{\partial z}$ and $\frac{\partial S}{\partial z}$ approach zero. Particularly the May to July

\bar{A}_s values are likely invalid because of the very small $\frac{\partial S}{\partial z}$.

The rapid influx of the cold water mass between July 31 and August 12 has been discussed qualitatively earlier. Its effect upon the \bar{A} computations is readily apparent. The character of this water mass as determined by the T - S relationships in the coastal water was approximately: temperature -1.2 to -1.3°C . and salinity 32.70 to 32.80‰. Thus it would seem likely that this water mass would interrupt the normal summer processes with a brief period of vertical convection. This convection might be visualized as taking place largely in the outer part of the fjord, the more saline water being transported to the inner part of the fjord by horizontal currents below sill depth. Evidence of some horizontal movement below sill depth is seen in the BT traces in Figure 5 which show the progressive intrusion of the cold water mass extending down to and projecting below the sill. \bar{A}_s values designated (X) are negative and therefore represent an impossible solution to the equation. At the times of each observation a positive $\frac{\partial S}{\partial z}$ slope is obtained, yet there is a net increase of salinity which must therefore have been caused by some process other than eddy diffusivity and is undoubtedly due to the intrusion of the cold more dense water and the temporary convection that has upset the normal summer processes. In fact the negative \bar{A}_s value and the low \bar{A}_T for the period July 9-31 at 100 m. are likely indications of the first effects of this water mass. Therefore the only reliable A_s values are considered to be over the period August to October.

The intrusion of the cold dense water that disrupted the A_s picture does not similarly affect the \bar{A}_T calculations. During the periods of observation $\frac{\partial T}{\partial z}$ is always negative with a normal corresponding rise in temperature of the bottom water. Since the temperature of this cold water was quite similar to that of the fjord water at the depths of calculation, the effects of the convection and horizontal currents are not apparent except in the case of the small \bar{A}_T factor at 60 m. between July 9 and August 12. The high \bar{A}_T value for the subsequent period may represent a compensating readjustment.

The unfortunate intrusion of the cold saline water mass at the time of the August observations, which has to a considerable extent obscured the turbulent processes, has limited the validity of the A calculations during this period. Of the values obtained it is felt that on the whole greater reliance may be placed on the temperature than on the salinity coefficients and that the A_T values obtained give us some general notion on the A factor as it applies to Hebron Fjord.

APPLICATION OF THE A FACTOR TO THE VERTICAL TRANSPORT OF DISSOLVED OXYGEN

During the summer months high oxygen content with supersaturation occurs in the upper layers with gradually decreasing amounts of oxygen toward the bottom. Therefore if downward mixing by turbulence occurs oxygen will be transported downward. However we note decreasing amounts of oxygen in the lower layers during the course of the summer. Thus the amount of oxygen consumed by biological respiration should equal the amount of oxygen transported downward by turbulence plus the net decrease of oxygen in these lower layers.

Calculations of the downward transport and consumption of dissolved oxygen have been made at station BD-130. A depth of 80 m. has been used in the calculations as it seems most suitable from the oxygen data available as well as the A_z values which are used, and it is below the euphotic zone. The quantity of oxygen (O) transported downward between the times t_1 and t_2 has been computed as follows:

$$O = -10^{-3} \int_{t_1}^{t_2} \bar{A} \frac{\partial O}{\partial z} dt$$

The results (upper two portions of Table X) are given in millilitres of oxygen transported through an area of cross-section of 1 cm.² during the two periods July 9-31 and from July 31 to August 12, and the quantities of oxygen are in a column of water of 1 cm.² cross-section from 80 m. to the bottom at 120 m.

The data in the upper two portions of Table X would appear to be of reasonable order of magnitude and indicate an uniform rate of oxygen consumption which might be expected with the uniformly cold water prevailing during the summer season in the lower levels. Biological activity may increase

TABLE X.—Calculations of vertical transport and consumption of oxygen in Hebron Fjord, 1954.

July 9 to July 31	
July 9 oxygen 80-120 m.	27.2 ml.
July 31 oxygen 80-120 m.	26.6 ml.
Net loss	0.6 ml.
Oxygen transported down ($A = 29$)	0.79 ml.
Total oxygen consumed	1.39 ml.
Av. rate of consumption	2.63×10^{-3} ml./hr.
July 31 to August 12	
July 31 oxygen 80-120 m.	26.6 ml.
Aug. 12 oxygen 80-120 m.	26.2 ml.
Net loss	0.4 ml.
Oxygen transported down ($A = 25$)	0.36 ml.
Total oxygen consumed	0.76 ml.
Av. rate of consumption	2.64×10^{-3} ml./hr.
August 12 to October 26	
Oxygen transported down ($A = 46$)	1.24 ml.
Total oxygen consumed (2.64×10^{-3} ml./hr.)	4.44 ml.
Net loss 80-120 m.	3.53 ml.
Reduction of oxygen 80-120 m. to	22.7 ml.
	or 5.67 ml./l.

somewhat during the late fall warming; however negative temperatures prevail in the lower levels throughout the annual cycle and such increase would likely be small.

The above calculations have been projected to October (lower portion of Table X), with the assumption that the uniform rate of oxygen consumption of summer is maintained throughout the fall.

Thus even if a greater oxygen consumption were encountered during the fall there would be no danger of oxygen depletion to a point of limiting biological activity, unless the process continues over a period of several years without any oxygen renewal. However, the uniformly high oxygen content observed over the several summers of observation suggests that complete renewal takes place during the winter processes of convection and exchange.

VI. DYNAMIC COMPUTATIONS

Some dynamic computations have been made from the Hebron station data. Specific volumes are expressed as the anomaly of the specific volume in situ and that of water of 35‰, 0°C. under atmospheric pressure (Δa). The dynamic height is then $D = \int_0^p \Delta a \, dp$. Various isobaric levels above 120 decibars, which was selected as a level of no motion, for the longitudinal section made August 11-12, 1954, are shown in Figure 19 as differences in dynamic millimetres as compared with station BD-133.

As would be expected the fjord water at this season lies at a higher level than the coastal water. The greatest height calculated is at BD-29 at all levels and not at the head of the fjord. This is easily explained by examining the principal fresh-water sources, which are not concentrated at the head of the fjord, but scattered from the head to Freytag Inlet; and hence the major proportion of run-off will pile up somewhere between BD-130 and BD-29.

On August 12 a section of five stations was made across the fjord including BD-130. The dynamic heights relative to 120 m. have been calculated, and the surface slope plotted (Fig. 20). Definite piling up of water is noted on the north shore, a lesser piling up on the south shore, and a low point at BD-135.

Calculation of the velocities at right angles to this section were made:

$$V - V_1 = \frac{10}{\lambda L} (D_A - D_B)$$

where D_A is the dynamic height for A, the left-hand, and D_B for B, the right-hand station, $\lambda = 2 \omega \sin \phi$ (ω being the angular velocity of the earth's rotation and ϕ the mean latitude), and L is the distance between stations. Lines of equal velocity are plotted in Figure 20 where the negative values (solid lines) are into the paper and positive values (dashed lines) are out.

To calculate the transports through the section the approximation of Theisen (1946) was used: a line some 30 to 40 m. above the bottom was drawn on the

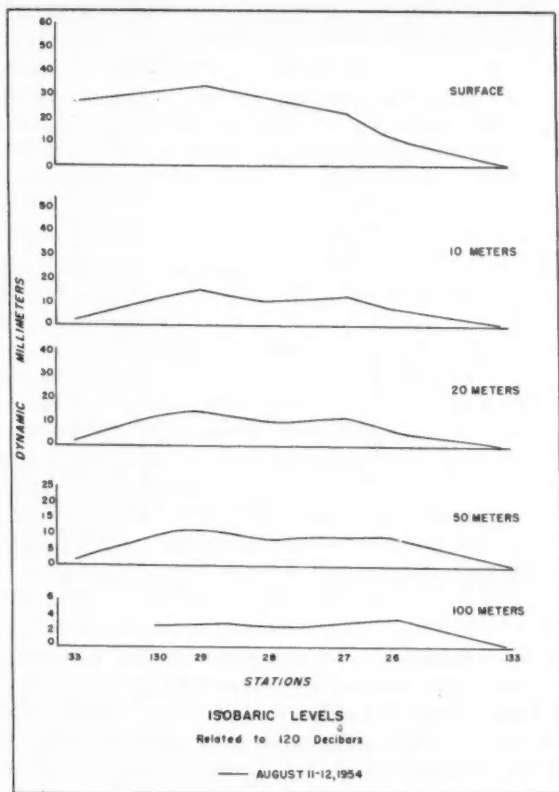


Figure 19.

velocity section, and the flows between this line and the bottom were neglected as being insignificant. The section was then planimeted, with the results:

Outflowing — 14,292 m.³/sec.

Inflowing — 17,498 m.³/sec.

Although the basic assumptions of no accelerations, no frictional forces, and a balance between pressure gradient and Coriolis force upon which dynamic computations are based, can at best only be partially fulfilled in confined coastal waters where fresh water mixing and tidal currents exist, it is interesting to see to what degree the dynamic picture agrees with the actual conditions as observed.

The pattern of velocity appears to indicate geostrophic movement with a strong inflow along the north shore and an outflow along the south shore. When the section was made, a sea breeze was blowing. Due to local topography the wind was only moderate along the south shore, while it freshened considerably

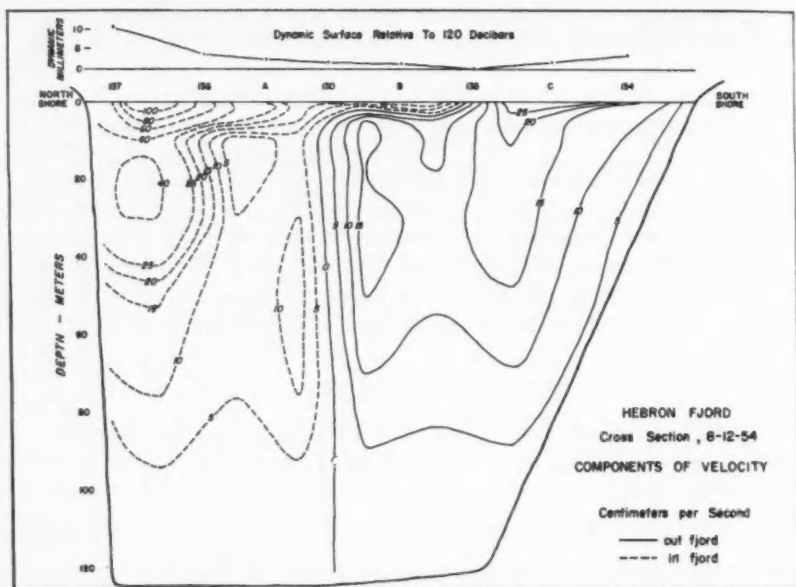


Figure 20.

toward the north shore. As the vessel was manoeuvred for the occupation of the three southern stations, little current was noted. During the occupation of the northern two stations, particularly BD-137 close by the north shore, a strong inflowing current was observed and estimated at about 2 knots, which is in reasonable agreement with the computed surface velocities.

At the time the section was made the tide was falling, which must have resulted in an actual seaward movement of water. The dynamic computations have shown a small net inflow. It would thus appear that although the values of transport obtained from the dynamic computations are not absolute, the qualitative description of the velocity pattern is in substantial agreement with the observed conditions.

VII. SUMMARY

1. Hebron Fjord, located at latitude $58^{\circ} 10' N.$ on the northeast coast of Labrador, is 255 m. deep with a 59-m. sill across its mouth. The climate and hydrological cycle of this area is sub-Arctic, with moderately cold winters which store all precipitation in the form of snow and ice, and moderately warm summers during which a large accumulation of fresh water from melting snow is released rapidly during the spring freshet. The volume of fresh-water contributions during the course of the annual cycle has been computed from the climatological data, watershed area, and ice cover.

2. During winter the waters within the fjord and immediate coastal water are uniformly isothermal and isohaline with a temperature of -1.76°C . and a salinity of 32.75‰. Soon after the advent of spring thaw about May 15 freshening and warming of the surface layers commence. The freshening takes place in advance of the warming and reaches a maximum in early July after which the fjord commences to salt. The maximum warming is not reached until sometime in September or early October. The drying up and freezing of the rivers in the fall, the formation of ice, and exchange with the coastal water lead to the re-establishment of isothermal and isohaline conditions during the ensuing winter.

During the last part of July and the first part of August 1954 a cold saline mass of water in passing along the coast from north to south invaded the fjord to upset the normal summer pattern.

3. A study of the temperature-salinity relationships more clearly defines the annual cycle and the relationships between the fjord and coastal water.

During winter the fjord and coastal waters become isothermal and isohaline with T - S relationships that may be identified as Arctic water of the Labrador Current. Due to the slow vertical exchange below sill depth after the establishment of a stable density gradient in summer the bottom water reflects essentially the conditions established during the preceding winter. Thus the condition of the bottom water during early and midsummer may be used as an indicator of the long-term trends of the Arctic water of the Labrador Current. The T - S relationships from the *Chance* data of 1926 and the *Blue Dolphin* data of 1949, 1952 and 1954 show a very slight warming trend, while a significant freshening is apparent. A correlation between these trends and recent changes in the Arctic Ocean and the Arctic-Atlantic circulation is suggested.

4. Ice formation as an oceanographic phenomenon is discussed. The thermohaline convection resulting from fall cooling and ice formation has been computed from the October 1954 data. It is shown that the inner fjord waters will freeze relatively early, while the freezing of the coastal water will be considerably delayed. In addition to the formation of ice a considerable exchange must take place between the fjord and coastal water to effect a return to the normal isothermal and isohaline conditions of mid winter. The thermal and haline cycles are considered in relation to both ice formation and exchange. It may be concluded that the formation and growth of ice is an important oceanographic feature of Arctic and sub-Arctic coastal waters.

5. The exchange mechanism and processes in Hebron Fjord may be described quite accurately qualitatively, but are difficult to determine quantitatively. Exchange is considered in essentially two parts, that above sill depth, which with free exchange between the fjord and coastal water involves principally horizontal movements, and that below sill depth which must involve vertical movements. Above sill depth, a slightly modified "steady state" concept is suggested which permits the calculation of a flushing time of approximately 68 days.

The bottom waters are not stagnant or dynamically dead, but enter into the exchange process at, however, a much slower rate. The waters below sill depth are renewed principally by vertical convection during winter. During

summer any exchange must overcome a stable density gradient and is accomplished by turbulence. Computations of the "Austausch" A factor of eddy conductivity and eddy diffusivity at and below sill depth show generally a larger A in spring and fall with a minimum in summer. A decreases with depth and distance from the source of energy which is primarily tidal action. Average A values of 67, 37 and 16 were obtained at the 60-, 80- and 100-m. levels respectively.

6. Dynamic heights determined in a longitudinal section show a pile-up of fresh water in the area where the greatest river flow is concentrated. Dynamic calculations of velocities and transport in a cross-section indicate a geostrophic flow. The calculated volumes of transport are not absolute, but the velocity pattern is in substantial agreement with observed conditions.

7. In Hebron Fjord a high Arctic marine environment exists during winter at all levels with a uniform temperature of -1.75°C . This high Arctic environment prevails throughout the annual cycle in the lower levels. At 100 m. the maximum temperature attained is barely -1.00°C ., while at 250 m. it has risen to only -1.68°C . In the upper levels above sill depth a significant seasonal amelioration takes place. This amelioration extends to greater depths in the coastal waters where negative temperatures have completely disappeared by mid-October down to 120 m., and likely deeper. Thus during the summer and fall seasons the bottom waters of Hebron Fjord become an isolated pocket of high Arctic marine environment.

Determinations of dissolved oxygen and inorganic phosphate content of the waters of Hebron Fjord have been made. In general there would appear to be an increase of phosphate content with depth. Photosynthetic activity maintains oxygen in the upper 30 m. at a level of supersaturation during the summer months. The rate of oxygen consumption below 80 m. has been computed from the amount of oxygen transported downward by eddy conductivity and the oxygen reduction observed in these levels during the summer months. It was found to be at a uniform rate of 2.64×10^{-3} ml./hr. in a column of water of 1 cm.² cross-section from 80 m. to the bottom at 120 m.

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STA. NO. <u>BD-27</u>	DATE <u>7/31/52</u>	TIME <u>0720</u>	ZONE <u>+ 3</u>
LAT. <u>58° 11.4' N</u>	LONG. <u>62° 34.2' W</u>	DEPTH <u>82</u> fms.	BT NO. <u>BD 4</u>
WEA. <u>Fine</u>	AIR TEMP. <u>48.3</u> °F.	WIND <u>N</u> <u>5</u> kts.	SECCHI <u>66</u> ft.
DEPTH m	TEMP. °C.	SAL. ‰	σ _t
0	6.1	28.82	22.69
5	5.86	29.69	23.42
10	4.31	30.91	24.54
20	2.08	31.69	25.34
30	1.21	31.87	25.55
50	0.08	32.10	25.79
100	-1.68	32.84	26.46
150	-1.72	32.90	26.49
REMARKS:			
STA. NO. <u>BD-28</u>	DATE <u>7/31/52</u>	TIME <u>0820</u>	ZONE <u>+ 3</u>
LAT. <u>58° 09.5' N</u>	LONG. <u>62° 45' W</u>	DEPTH <u>143</u> fms.	BT NO. <u>BD 4</u>
WEA. <u>Fine</u>	AIR TEMP. <u>55.0</u> °F.	WIND <u>SE</u> <u>6</u> kts.	SECCHI <u>65</u> ft.
DEPTH m	TEMP. °C.	SAL. ‰	σ _t
0	7.5	27.83	21.75
5	5.26	30.01	23.73
10	3.19	31.08	24.77
20	2.09	31.69	25.34
30	1.21	31.84	25.63
50	0.15	32.03	25.87
100	-1.69	32.83	26.43
150	-1.73	32.86	26.46
200	-1.69	32.86	26.45
250	-1.74	32.88	26.48
REMARKS:			
STA. NO. <u>BD-29</u>	DATE <u>7/31/52</u>	TIME <u>1110</u>	ZONE <u>+ 3</u>
LAT. <u>58° 08.2' N</u>	LONG. <u>62° 55.3' W</u>	DEPTH <u>98</u> fms.	BT NO. <u>BD 4</u>
WEA. <u>Fine</u>	AIR TEMP. <u>50.0</u> °F.	WIND <u>light variable</u>	SECCHI <u>70</u> ft.
DEPTH m	TEMP. °C.	SAL. ‰	σ _t
0	6.7	27.75	21.81
5	4.72	30.17	23.91
10	2.71	31.38	25.05
20	2.07	31.65	25.32
30	1.21	31.84	25.58
50	-1.10	32.11	25.72
100	-1.67	32.75	26.37
150	-1.71	32.79	26.41
REMARKS:			
STA. NO. <u>BD-26</u>	DATE <u>3/24/54</u>	TIME <u>1330</u>	ZONE <u>+ 4</u>
LAT. <u>58° 14.2' N</u>	LONG. <u>62° 29.0' W</u>	DEPTH <u>62</u> fms.	BT NO. <u>BD 12</u>
WEA. <u>Fine</u>	AIR TEMP. <u>5</u> °F.	WIND <u>W</u> <u>3</u> kts.	SECCHI <u>—</u> ft.
DEPTH m	TEMP. °C.	SAL. ‰	σ _t
0	-1.67	32.75	26.38
5	-1.77	32.76	26.38
10	-1.78	32.75	26.38
20	-1.78	32.75	26.39
30	-1.79	32.76	26.39
50	-1.78	32.76	26.39
100	-1.78	32.77	26.39
REMARKS: Snow cover - 0 Ice thickness - 16"			
STA. NO. <u>BD-28</u>	DATE <u>3/29/54</u>	TIME <u>1330</u>	ZONE <u>+ 4</u>
LAT. <u>58° 09.5' N</u>	LONG. <u>62° 45.0' W</u>	DEPTH <u>143</u> fms.	BT NO. <u>BD 12</u>
WEA. <u>Unsettled</u>	AIR TEMP. <u>4</u> °F.	WIND <u>NE</u> <u>5</u> kts.	SECCHI <u>—</u> ft.
DEPTH m	TEMP. °C.	SAL. ‰	σ _t
0	-1.67	32.79	26.41
5	-1.75	32.75	26.40
10	-1.75	32.75	26.38
20	-1.75	32.75	26.38
30	-1.75	32.75	26.38
50	-1.75	32.75	26.38
100	-1.75	32.75	26.38
150	-1.74	32.75	26.38
200	-1.77	32.75	26.38
250	-1.75	32.75	26.38
REMARKS: Snow cover - 10" - 12" Ice thickness - 33"			
STA. NO. <u>BD-30</u>	DATE <u>4/7/54</u>	TIME <u>1330</u>	ZONE <u>+ 4</u>
LAT. <u>58° 04.2' N</u>	LONG. <u>63° 06.0' W</u>	DEPTH <u>—</u> fms.	BT NO. <u>BD 12</u>
WEA. <u>Fine</u>	AIR TEMP. <u>8.5</u> °F.	WIND <u>W</u> <u>5</u> kts.	SECCHI <u>—</u> ft.
DEPTH m	TEMP. °C.	SAL. ‰	σ _t
0	-1.67	32.77	26.39
5	-1.76	32.72	26.35
10	-1.76	32.72	26.35
20	-1.75	32.74	26.36
30	-1.76	32.72	26.35
50	-1.77	32.72	26.35
100	-1.74	32.74	26.36
REMARKS: Snow cover - 24" Ice thickness - 47"			

STA. NO.	HD-130	DATE	7/2/54	TIME	1600	ZONE	+ 3
LAT.	58° 00.5' N	LONG.	63° 00.4' W	DEPTH	68	Fm.	BT NO. HD 12, 102
WEA.	Fine	AIR TEMP.	50.1	OP.	WIND	5 kts.	SECCHI 25 ft.
DEPTH m	TEMP °C.	SAL.	°/100	σ _t	O ₂ ml/L	PQ ₀ μg/L	
0	5.9	28.64	22.58	7.70	0.17		
5	5.72	28.66	22.61	7.81	0.22		
10	3.79	29.58	23.58	8.50	0.22		
20	0.95	31.55	25.29	9.05	0.33		
30	0.44	31.65	25.41	8.66	0.54		
40	-0.56	32.10	25.81	8.86	0.68		
100	-1.72	32.65	26.25	6.73	1.12		

REMARKS:

STA. NO.	HD-31	DATE	7/2/54	TIME	1500	ZONE	+ 3
LAT.	58° 01.5' N	LONG.	63° 08.0' W	DEPTH	43	Fm.	BT NO. HD 12, 108
WEA.	Fine	AIR TEMP.	55.8	OP.	WIND	NNW 7 kts.	SECCHI 20 ft.
DEPTH m	TEMP °C.	SAL.	°/100	σ _t	O ₂ ml/L	PQ ₀ μg/L	
0	6.2	27.11	21.33				
5	5.34	27.63	21.83				
10	2.84	30.08	24.01				
20	0.00	31.20	25.60				
30	-1.04	32.25	25.95				
50	-1.62	32.41	26.09				
75	-1.73	32.57	26.23				

REMARKS:

STA. NO.	HD-29	DATE	7/10/54	TIME	0530	ZONE	+ 3
LAT.	58° 08.5' N	LONG.	62° 55.2' W	DEPTH	100	Fm.	BT NO. HD 12, 109
WEA.	Fine	AIR TEMP.	45.0	OP.	WIND	M	SECCHI 22 ft.
DEPTH m	TEMP °C.	SAL.	°/100	σ _t	O ₂ ml/L	PQ ₀ μg/L	
0	5.8	28.87	22.78				
5	5.44	28.93	22.85				
10	2.05	30.75	24.60				
20	1.04	31.38	25.16				
30	0.26	32.28	25.32				
40	-0.87	32.38	25.31				
100	-1.74	32.57	26.23				
150	-1.76	32.70	26.33				
180	-1.76	32.70	26.33				

REMARKS:

STA. NO.	HD-28	DATE	7/10/54	TIME	0800	ZONE	+ 3
LAT.	58° 09.5' N	LONG.	62° 45.0' W	DEPTH	143	Fm.	BT NO. HD 12, 110
WEA.	Fine	AIR TEMP.	44.2	OP.	WIND	M	SECCHI 31 ft.
DEPTH m	TEMP °C.	SAL.	°/100	σ _t	O ₂ ml/L	PQ ₀ μg/L	
0	3.3	28.36	23.40				
5	3.34	30.28	24.12				
10	1.56	30.93	24.77				
20	1.46	31.31	25.08				
30	0.12	32.20	25.80				
40	-1.71	32.66	26.30				
100	-1.75	32.68	26.32				
150	-1.76	32.70	26.33				
200	-1.75	32.70	26.33				
250	-1.75	32.70	26.33				

REMARKS:

STA. NO.	HD-27	DATE	7/10/54	TIME	1215	ZONE	+ 3
LAT.	58° 11.5' N	LONG.	62° 34.2' W	DEPTH	99	Fm.	BT NO. HD 12, 111
WEA.	Fine	AIR TEMP.	51.0	OP.	WIND	Calm	SECCHI 33 ft.
DEPTH m	TEMP °C.	SAL.	°/100	σ _t	O ₂ ml/L	PQ ₀ μg/L	
0	2.6	30.21	24.12				
5	1.00	30.30	24.29				
10	-1.18	30.77	24.72				
20	0.20	31.11	24.99				
30	-0.08	31.46	25.27				
50	-0.57	32.08	25.80				
100	-1.11	32.61	26.33				
150	-1.71	32.70	26.33				
175	-1.73	32.74	26.36				

REMARKS: Moored to ice pan

STA. NO.	HD-26	DATE	7/10/54	TIME	1415	ZONE	+ 3
LAT.	58° 14.2' N	LONG.	62° 29.0' W	DEPTH	64	Fm.	BT NO. HD 12, 112
WEA.	Fine	AIR TEMP.	49.1	OP.	WIND	Calm	SECCHI 20 ft.
DEPTH m	TEMP °C.	SAL.	°/100	σ _t	O ₂ ml/L	PQ ₀ μg/L	
0	2.5	29.38	23.47				
5	-0.05	30.41	24.43				
10	0.05	30.73	24.69				
20	-0.19	31.26	25.12				
30	-0.06	31.51	25.32				
50	-0.68	31.63	25.60				
100	-1.25	32.46	26.14				

REMARKS: Moored to ice pan

STA. NO. <u>BD-130</u>	DATE <u>7/31/54</u>	TIME <u>1430</u>	ZONE <u>+ 3</u>
LAT. <u>58.0</u> <u>04.2</u> 'N	LONG. <u>62.0</u> <u>10.8</u> 'W	DEPTH <u>68</u> fms.	BT NO. <u>BD 12</u> <u>157</u>
WEA. <u>Overcast</u>	AIR TEMP. <u>50.5</u> °F	WIND <u>E</u> <u>5</u> kts.	SECCHI <u>26</u> ft.
DEPTH m	TEMP. °C	SAL. ‰	σ _t
0	9.0	34.65	18.05
5	8.09	35.73	24.77
10	1.70	35.55	25.38
20	0.88	35.58	25.80
30	0.41	35.63	26.18
40	-0.63	35.62	26.63
80	-1.29	35.47	26.05
110	-1.71	35.69	26.22
PO ₄ μg/L	O ₂ ml/L	σ _t	PO ₄ μg/L
0	---	---	---
5	---	---	---
10	---	---	---
20	---	---	---
30	---	---	---
40	---	---	---
80	---	---	---
110	---	---	---
REMARKS:			

STA. NO. <u>BD-133</u>	DATE <u>8/3/54</u>	TIME <u>1400</u>	ZONE <u>+ 3</u>
LAT. <u>58.0</u> <u>16</u> 'N	LONG. <u>62.0</u> <u>10</u> 'W	DEPTH <u>115</u> fms.	BT NO. <u>BD 12</u> <u>150</u>
WEA. <u>Fine</u>	AIR TEMP. <u>51.4</u> °F	WIND <u>Caln</u> <u>1</u> kts.	SECCHI <u>13</u> ft.
DEPTH m	TEMP. °C	SAL. ‰	σ _t
0	2.2	30.88	24.94
5	1.21	31.58	25.43
10	0.71	31.74	25.53
20	0.23	31.85	25.62
30	0.13	31.85	25.62
40	-0.13	32.50	26.07
50	-1.13	32.84	26.34
100	-1.30	32.84	26.34
150	-1.33	32.92	26.40
PO ₄ μg/L	O ₂ ml/L	σ _t	PO ₄ μg/L
0	0.15	0.84	---
5	0.40	0.71	---
10	0.95	0.43	---
20	0.76	0.31	---
30	-0.87	0.21	---
40	-0.58	0.30	---
50	-0.58	0.30	---
100	-1.64	0.32	---
150	-1.71	0.32	---
REMARKS:			

STA. NO. <u>BD-133</u>	DATE <u>8/11/54</u>	TIME <u>1435</u>	ZONE <u>+ 3</u>
LAT. <u>58.0</u> <u>11.5</u> 'N	LONG. <u>62.0</u> <u>34.2</u> 'W	DEPTH <u>99</u> fms.	BT NO. <u>BD 12</u> <u>158</u>
WEA. <u>Cloudy</u>	AIR TEMP. <u>53.1</u> °F	WIND <u>NNE</u> <u>3</u> kts.	SECCHI <u>46</u> ft.
DEPTH m	TEMP. °C	SAL. ‰	σ _t
0	9.2	26.29	20.32
5	0.91	31.44	25.22
10	0.53	31.53	25.43
20	-0.76	31.92	25.75
30	-0.87	32.01	25.75
40	-0.87	32.30	25.97
50	-0.58	32.30	25.97
100	-1.64	32.72	26.35
150	-1.71	32.72	26.35
175	-1.70	32.77	26.39
PO ₄ μg/L	O ₂ ml/L	σ _t	PO ₄ μg/L
0	---	---	---
5	---	---	---
10	---	---	---
20	---	---	---
30	---	---	---
40	---	---	---
50	---	---	---
100	---	---	---
150	---	---	---
175	---	---	---
REMARKS:			

STA. NO. <u>BD-28</u>	DATE <u>8/12/54</u>	TIME <u>1045</u>	ZONE <u>+ 3</u>
LAT. <u>58.0</u> <u>09.5</u> 'N	LONG. <u>62.0</u> <u>45.0</u> 'W	DEPTH <u>143</u> fms.	BT NO. <u>BD 12</u> <u>159</u>
WEA. <u>Fine</u>	AIR TEMP. <u>49.0</u> °F	WIND <u>SE</u> <u>5</u> kts.	SECCHI <u>47</u> ft.
DEPTH m	TEMP. °C	SAL. ‰	σ _t
0	10.8	23.30	17.75
5	1.62	31.35	25.09
10	-0.02	31.78	25.53
20	---	31.96	---
30	-0.62	32.16	25.88
40	-0.99	32.29	25.98
50	-1.12	32.37	26.16
100	-1.72	32.75	26.38
150	-1.74	32.77	26.39
250	-1.74	32.75	26.38
PO ₄ μg/L	O ₂ ml/L	σ _t	PO ₄ μg/L
0	---	---	---
5	---	---	---
10	---	---	---
20	---	---	---
30	---	---	---
40	---	---	---
50	---	---	---
100	---	---	---
150	---	---	---
250	---	---	---
REMARKS:			

STA. NO.	HD-29	DATE	8/12/54	TIME	0915	ZONE	+ 3
LAT.	58° 00.5' N	LONG.	62° 03.2' W	DEPTH	100 fms.	BT NO.	HD 12, 160
WEA.	Cloudy	AIR TEMP.	51.9 °F	WIND	SE 5 kts.	SECCHI	30 ft.
DEPTH	TEMP °C.	SAL.	O/∞	σ _t	O ₂ ml/L	PO ₄ μM/L	
0	11.1	22.14	16.82				
5	1.71	31.42	25.15				
10	0.79	31.74	25.46				
20	-1.10	31.62	25.63				
30	-1.76	32.07	25.80				
40	-2.24	32.41	26.01				
100	-1.67	32.70	26.33				
150	-1.74	32.75	26.38				
180	-1.78	32.75	26.38				
REMARKS:							
STA. NO.	HD-134	DATE	8/12/54	TIME	1015	ZONE	+ 3
LAT.	58° 06.1' N	LONG.	62° 59.5' W	DEPTH	22 fms.	BT NO.	HD 12, 161
WEA.	Fine	AIR TEMP.	50.0 °F	WIND	E 5 kts.	SECCHI	41 ft.
DEPTH	TEMP °C.	SAL.	O/∞	σ _t	O ₂ ml/L	PO ₄ μM/L	
0	11.1	22.07	16.76				
5	2.04	31.42	25.13				
10	0.74	31.62	25.46				
20	-1.38	31.98	25.71				
30	-1.60	32.12	25.83				
REMARKS:							
STA. NO.	HD-135	DATE	8/12/54	TIME	1040	ZONE	+ 3
LAT.	58° 06.3' N	LONG.	63° 00.2' W	DEPTH	66 fms.	BT NO.	HD 12, 162
WEA.	Fine	AIR TEMP.	57.5 °F	WIND	E 10 kts.	SECCHI	41 ft.
DEPTH	TEMP °C.	SAL.	O/∞	σ _t	O ₂ ml/L	PO ₄ μM/L	
0	8.3	22.41	17.41				
5	1.55	31.38	25.13				
10	0.28	31.74	25.48				
20	-1.37	32.00	25.72				
30	-1.88	32.12	25.84				
40	-2.11	32.21	25.91				
100	-1.57	32.65	26.28				
REMARKS:							

STA. NO.	HD-130	DATE	8/12/54	TIME	1105	ZONE	+ 3
LAT.	58° 06.6' N	LONG.	63° 00.8' W	DEPTH	68 fms.	BT NO.	HD 12, 163
WEA.	Fine	AIR TEMP.	56.5 °F	WIND	E 10 kts.	SECCHI	41 ft.
DEPTH	TEMP °C.	SAL.	O/∞	σ _t	O ₂ ml/L	PO ₄ μM/L	
0	10.0	21.51	19.36				
5	1.96	31.27	25.02				
10	0.57	31.80	25.52				
20	-1.42	31.94	25.68				
30	-1.74	32.12	25.84				
40	-1.88	32.29	25.96				
100	-1.61	32.65	26.28				
120	-1.70	32.75	26.38				
REMARKS:							
STA. NO.	HD-136	DATE	8/12/54	TIME	1135	ZONE	+ 3
LAT.	58° 06.8' N	LONG.	63° 01.3' W	DEPTH	68 fms.	BT NO.	HD 12, 164
WEA.	Fine	AIR TEMP.	57.0 °F	WIND	E 12 kts.	SECCHI	41 ft.
DEPTH	TEMP °C.	SAL.	O/∞	σ _t	O ₂ ml/L	PO ₄ μM/L	
0	9.9	21.82	16.72				
5	3.46	30.72	24.46				
10	0.48	31.80	25.52				
20	-1.33	31.98	25.70				
30	-1.63	32.14	25.85				
40	-1.91	32.29	25.98				
100	-1.61	32.65	26.28				
REMARKS:							
STA. NO.	HD-137	DATE	8/12/54	TIME	1205	ZONE	+ 3
LAT.	58° 06.9' N	LONG.	63° 01.8' W	DEPTH	68 fms.	BT NO.	HD 12, 165
WEA.	Fine	AIR TEMP.	55.7 °F	WIND	E 10 kts.	SECCHI	41 ft.
DEPTH	TEMP °C.	SAL.	O/∞	σ _t	O ₂ ml/L	PO ₄ μM/L	
0	8.8	21.58	16.73				
5	4.43	29.42	23.34				
10	0.22	31.87	25.60				
20	-1.42	32.01	25.74				
30	-1.65	32.10	25.81				
40	-1.93	32.30	25.98				
REMARKS:							

STA. NO. HD-13	DATE 8/12/54	TIME 1310	ZONE + 3
LAT. 58° 00.5' N	LONG. 63° 00.0' W	DEPTH 43 fms.	BT NO. HD 12, 146
WEA. Fine	AIR TEMP. 64.6 °F	WIND N 7 kts.	SECCHI 62 ft.
DEPTH m	TEMP. °C	SAL. ‰	σ _t
0	8.57	35.23	18.25
5	10.17	35.22	18.27
10	0.82	31.71	25.43
20	0.10	31.96	25.67
30	- .29	32.07	25.78
50	-1.46	32.63	26.27
75	-1.68	32.68	26.32
REMARKS:			

STA. NO. HD-26	DATE 10/15/54	TIME 1300	ZONE + 31
LAT. 58° 14.2' N	LONG. 62° 29.0' W	DEPTH 64 fms.	BT NO. HD 12, 254
WEA. Overcast	AIR TEMP. 37.7 °F	WIND Calm	SECCHI --- ft.
DEPTH m	TEMP. °C	SAL. ‰	σ _t
0	1.6	---	---
5	1.52	32.07	25.69
10	1.48	32.12	25.73
20	1.36	32.23	25.83
50	1.09	32.32	25.92
100	0.38	---	---
REMARKS:			

STA. NO. HD-28	DATE 10/18/54	TIME 1230	ZONE + 31
LAT. 58° 09.5' N	LONG. 62° 45.0' W	DEPTH 143 fms.	BT NO. HD 12, 255
WEA. Mild	AIR TEMP. 43.5 °F	WIND N 5 kts.	SECCHI --- ft.
DEPTH m	TEMP. °C	SAL. ‰	σ _t
0	1.7	31.42	25.15
5	1.67	31.58	25.28
10	1.60	---	---
20	1.47	32.08	25.70
30	1.27	32.10	25.73
50	0.68	32.33	25.94
100	-1.01	32.62	26.25
150	-1.51	32.69	26.32
200	-1.63	32.75	26.38
250	-1.68	32.76	26.39
REMARKS:			

STA. NO. HD-130	DATE 10/26/54	TIME 1430	ZONE + 33
LAT. 58° 05.6' N	LONG. 63° 00.8' W	DEPTH 68 fms.	BT NO. HD 12, 257
WEA. Fine	AIR TEMP. 30.8 °F	WIND NW 10 kts.	SECCHI --- ft.
DEPTH m	TEMP. °C	SAL. ‰	σ _t
0	0.00	31.16	25.03
5	0.35	31.38	25.19
10	0.51	31.57	25.35
20	0.65	32.20	25.83
30	0.50	32.25	25.88
50	0.01	32.36	26.00
100	- .98	32.51	26.10
REMARKS:			

STA. NO. _____	DATE _____	TIME _____	ZONE + _____
LAT. _____ ° _____ ' N	LONG. _____ ° _____ ' W	DEPTH _____ fms.	BT NO. _____
WEA. _____	AIR TEMP. _____ °F	WIND _____ kts.	SECCHI _____ ft.
DEPTH m	TEMP. °C	SAL. ‰	σ _t
			O ₂ ml/l
			PO ₄ μg/l
REMARKS:			

STA. NO. _____	DATE _____	TIME _____	ZONE + _____
LAT. _____ ° _____ ' N	LONG. _____ ° _____ ' W	DEPTH _____ fms.	BT NO. _____
WEA. _____	AIR TEMP. _____ °F	WIND _____ kts.	SECCHI _____ ft.
DEPTH m	TEMP. °C	SAL. ‰	σ _t
			O ₂ ml/l
			PO ₄ μg/l
REMARKS:			

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